THE

SYDENHAM SOCIETY

INSTITUTED

MDCCCXLIII.

LONDON

MDCCCLIII.

MANUAL

OF

HUMAN HISTOLOGY.

BY

A. KÖLLIKER,

PROFESSOR OF ANATOMY AND PHYSIOLOGY IN WURZBURG.

TRANSLATED AND EDITED

BY

GEORGE BUSK, F.R.S., AND THOMAS HUXLEY, F.R.S.

VOLUME 1.

LONDON:

PRINTED FOR THE SYDENHAM SOCIETY.

MDCCCLIII.

PRINTED BY C. AND J. ADLARD,
BARTHOLOMEW CLOSE.

AUTHOR'S PREFACE.

MEDICINE has reached a point, at which Microscopical Anatomy appears to constitute its foundation, quite as much as the Anatomy of the Organs and Systems; and when a profound study of Physiology and Pathological Anatomy is impossible, without an accurate acquaintance also, with the most minute structural conditions. It seems, therefore, to be the task of the cultivators of this branch of science, to communicate the results of their researches, not only to their fellow inquirers, and to those who have, in other ways, gone more deeply into medical science, but to all who are devoted to the study of Man in general, and especially to render them easily available by students and practitioners. The attainment of this object is sought, in the present work, by giving a view, as condensed as possible, of the relations of the elementary parts of the body, and of the more intimate structure of the organs. In the execution of this plan, with the exception of some important, but still doubtful questions, all polemical disquisition is avoided, and the History of the Science also left altogether in the background; whilst as constant

reference as could in any way be admitted, has been made to Physiology and Pathological Anatomy, as well as to Comparative Histology.

For further information, the Author refers to more detailed Anatomical works, and particularly to his 'Microscopical Anatomy,' in which the *data* for all that is here only briefly expressed, will be found.

WURZBURG; *August 1st*, 1852.

TRANSLATORS' PREFACE.

The Translators feel that an English edition of a book, which has justly taken so high a position as Professor Kölliker's 'Manual of Human Histology,' needs no lengthened introduction to the members of the Sydenham Society.

In the rendering of the work they have endeavoured to follow faithfully the text of the 'Handbuch der Gewebelehre,' with the occasional incorporation, however, of a few sentences from the larger 'Mikroskopische Anatomie,' by the same Author, where it appeared to them that the more condensed style of the present work had rendered the sense less clear than was desirable. They have also added, in the shape of notes (distinguished by a smaller type), whatever comments of their own seemed to be called for. But the short time allowed by circumstances for the publication of the present volume (which includes the first half of the original), having prevented their making these notes so full, or so numerous, as might have been desired upon several subjects, and particularly on the general doctrine of the Cell, the Translators propose to

add such additional Commentary as they may have to offer, in a "General Appendix" at the end of the work.

No alteration has been made in the expression of the measurements, for which the Paris line, equal to about $\frac{1}{11}$th (0·0888138) of an English inch (and now very generally adopted on the continent), is taken as the unit; nor in the signs ‴ for 'of a line,' and ″ for 'of an inch,' the great convenience of which will probably lead to their more general acceptance.

LONDON; *August 1st*, 1853

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INTRODUCTION.

§ 1.

THE doctrine of the elementary structure of Plants and Animals, belongs to the last two centuries, originating with Marcellus Malpighi (1628-94), and Anton van Leeuwenhoek (1632-1723), at the period when the assistance of magnifying glasses, powerful, though of very simple form, was first offered to observers. The ultimate constituents in respect of form, of organisms, were unknown to antiquity and to the middle ages, for although Aristotle and Galen speak of the homogeneous and heterogeneous parts of the body (partes similares et dissimilares), and Fallopius (1523-62) defined still more exactly the idea of "Tissues," and even attempted to classify them, ('Tractatus quinque de partibus similaribus,' opera, tom. ii, Francof. 1600), yet the minuter structures were completely hidden from these investigators. Brilliant as were the first efforts of young science under the guidance of these men and afterwards of a Ruysch, Swammerdam and others, yet they were not adequate to acquire a safe footing for it, since, on the one hand, the philosophers were far too little masters of microscopic investigation to strive at once, with clear insight, towards the true goal; while, on the other, the development of other branches of study, as of the grosser Anatomy, of Physiology, of Embryology and of Comparative Anatomy, claimed too large a share of their attention. It thus happened that, with the exception of a few to some extent important works

(Fontana, Muys, Lieberkühn, Hewson, Prochaska), Histology made no considerable progress during the whole of the 18th century, and acquired no importance greater than that due to a disjointed collection of isolated observations. It was in the year 1801 that it first acquired a rank co-equal with that of its sister anatomical sciences, by the genius of a man to whom indeed, Histology owes no great discoveries, but who understood, as no one before him had done, so to arrange existing materials and so to connect them with Physiology and Medicine, that for the future its independence was assured. In fact, Bichat's 'Anatomie Générale' (Paris, 1801), was the first attempt to treat Histology scientifically, and on this account merely, it constitutes an epoch; but besides this, its importance was still greater, inasmuch as the tissues were not merely clearly defined and fully and logically treated of, but full account was taken of their physiological functions and morbid alterations. To this great internal progress, the present century has added an ever-increasing perfection of the external aids of the microscope, and a steadily increasing zeal in the investigation of nature, so that it is not to be wondered at, that in its five decades, it has left far behind all that was done in the century and a half of its earlier existence. In the last thirty years particularly, discoveries have so trodden upon one another's heels, that it must be considered truly fortunate that a bond of connection has arisen, and that Microscopical Anatomy has thus escaped the danger of becoming, as in earlier days, lost in minutiæ. In the year 1838, in fact, the demonstration by Dr. Th. Schwann, of the originally perfectly identical cellular composition of all animal organisms, and of the origin of their higher structures from these elements, afforded the appropriate conception which united all previous observations, and afforded a clue for further investigations. If Bichat founded histology more theoretically by constructing a system and carrying it out logically, Schwann has, by his investigations, afforded a basis of fact, and has thus won the second laurels in this field. What has been done in this science since Schwann, has been indeed of great importance to physiology and medicine, and in part of great value in a purely scientific point of view, inasmuch as a great deal which Schwann only indicated, or shortly adverted to, as the genesis of the cell, the

import of the nucleus, the development of the higher tissues, their chemical relations, &c., has received a further development; but all this has not amounted to a step so greatly in advance as to constitute a new epoch. If, without pretensions to prescience, it be permitted to speak of the future, this condition of histology will last as long as no essential advance is made towards penetrating more deeply into organic structure, and becoming acquainted with those elements of which that which we at present hold to be simple, is composed. If it be possible that the molecules which constitute cell-membranes, muscular fibrils, axile fibre of nerves, &c., should be discovered, and the laws of their apposition, and of the alterations which they undergo in the course of the origin, the growth, and the activity of the present so-called elementary parts, should be made out, then a new era will commence for Histology, and the discoverer of the law of *cell genesis*, or of a *molecular theory*, will be as much or more celebrated than the originator of the doctrine of the composition of all animal tissues out of cells.

§ 2.

In characterising the present position of Histology and of its *objects*, we must by no means forget that, properly speaking, it considers only one of the three aspects which the elementary parts present to observation, namely, their form. Microscopical anatomy is concerned with the understanding of the microscopic forms, and with the laws of their structure and development, not with any general doctrine of the elementary parts. Composition and function are only involved, so far as they relate to the origin of forms and to their variety. Whatever else respecting the activity of the perfect elements and their chemical relations is to be found in Histology, is there either on practical grounds in order to give some useful application of the morphological conditions, or to complete them; or from its intimate alliance with the subject, it is added only because physiology proper does not afford a due place for the functions of the elementary parts.

If Histology is to attain the rank of a science, its first need is to have as broad and certain an objective basis as possible. To this end, the minuter structural characters of animal organisms

are to be examined on all sides and not only in fully-formed structures, but in all the earlier periods from their first development. When the morphological elements have been perfectly made out, the next object is to discover the laws according to which they arise, wherein one must not fail to have regard also to their relations of composition and function. In discovering these laws, here as in the experimental sciences generally, continual observation separates more and more, among the collective mass of scattered facts and observations, the occasional from the constant, the accidental from the essential, till at last a series of more and more general expressions of the facts arises,—from which, in the end, mathematical expressions or formulæ proceed, and thus the laws are enunciated.

If we inquire how far Histology has satisfied these requirements, and what are its prospects in the immediate future, the answer must be a modest one. *Not only does it not possess a single law,* but the materials at hand from which such should be deduced, are as yet relatively so scanty, that not even any considerable number of general propositions appear well founded. Not to speak of a complete knowledge of the minuter structure of animals in general, we are not acquainted with the structure of a single creature throughout, not even of man, although he has been so frequently the object of investigation,—and therefore it has hitherto been impossible to bring the science essentially any nearer its goal. It would, however, be unjust to overlook and depreciate what we do possess; and it may at any rate be said, that we have acquired a rich store of facts and a few more trustworthy general propositions. To indicate only the more important of the former, it may be mentioned, that we have a very sufficient acquaintance with the perfect elementary parts of the higher animals and that we also understand their development, with the exception of the elastic tissue, and of the elements of the teeth and bones. The mode in which these are united into organs has been less examined, yet on this head also, much has been added of late, especially in man, whose individual organs with the exception of the nervous system, the higher organs of sense and a few glands (the liver, blood-vascular glands), have been almost exhaustively investigated. If the like progress continue to

be made, the structure of the human body will in a few years be so clearly made out, that, except perhaps in the nervous system, nothing more of importance will remain to be done with our present modes of investigation. With comparative Histology it is otherwise; hardly commenced, not years but decades will be needed to carry out the necessary investigations. Whoever will do good work in this field must, by monographs of typical forms embracing their whole structure from the earliest periods of development,[1] obtain a general view of all the divisions of the animal kingdom, and then, by the methods above described, strive to develop their laws.

As regards the general propositions of Histology, the science has made no important progress since Schwann, however much has been attained by the confirmation of the broad outlines of his doctrines. The position that all the higher animals at one time consist wholly of cells and develop from these their higher elementary parts, stands firm, though it must not be understood as if cells, or their derivatives, were the sole possible or existing elements of animals. In the same way, Schwann's conception of the genesis of cells, though considerably modified and extended, has not been essentially changed, since the cell nucleus still remains as the principal factor of cell development and of cell multiplication. Least advance has been made in the laws which regulate the origin of cells and of the higher elements, and our acquaintance with the elementary processes which take place during the formation of organs must be regarded as very slight. Yet the right track in clearing up these points has been entered upon; and a logical investigation of *the chemical relations of the elementary parts and of their molecular forces*, after the manner of Donders, Dubois, Ludwig, and others, combined with a more *profound microscopical examination* of them, such as has already taken place with regard to the muscles and nerves,—further, a histological treatment of embryology, such as has been attempted by Reichert, Vogt and myself, will assuredly raise the veil, and bring us, step by step, nearer to the desired though perhaps never to be reached, end.

[[1] See a very praiseworthy monograph of this kind by Leydig, Beiträge zur Mikroskopischen Anatomie und Entwickelungs-geschichte der Rochen u. Haie, 1852. (Microscopic Anatomy and Development of the Rays and Sharks.)—Eds.]

§ 3.

The *aids* in studying histology may here be best shortly adverted to. With respect to the *literature* of the subject, the more important monographic works are cited under their appropriate section, and here only those large independent works will be noticed, in which further instruction is to be found. It is right to head the list with Schwann's 'Mikroskopische Untersuchungen über die Uebereinstimmung in der Struktur und dem Wachsthum der Thiere und Pflanzen' (Berlin, 1839),[1] abstracted in Froriep's 'Neue Notizen' (1838), as the most fitting introduction to Histology. Beside this, we may name X. Bichat, 'Anatomie Générale,' Tom. iv (Paris, 1801); E. H. Weber, 'Handbuch der Anatomie des Menschen von Hildebrandt,' Bd. 1, 'Allgemeine Anatomie' (Braunschweig, 1830), a work distinguished in its day, and even now indispensably necessary, as a store of old literature, [or Ed. 4 (Stuttgart, 1833)]; Brun's 'Lehrbuch der Allgemeinen Anatomie des Menschen' (Braunschweig, 1841), very clear, concise and good; Henle, 'Allgemeine Anatomie' (Leipzig, 1841), containing a classical account of Histology in the year 1840, many original statements, and physiological, pathological, and historical remarks; G. Valentin, article 'Gewebe,' in R. Wagner's 'Handwörterbuch d. Physiologie,' Bd. i (1842); R. B. Todd and W. Bowman, 'The Physiological Anatomy and Physiology of Man,' Parts i, ii (London, 1845-47), mostly based upon original observations, very comprehensive and good, [also Parts iii, iv (1847-52)]; Bendz, 'Haandbog i den almindelige Anatomie' (Kiöbenhavn, 1846-47), with industriously collected historical data; A. Kölliker, 'Mikroskopische Anatomie oder Gewebelehre des Menschen, Band II, Specielle Gewebelehre, 1. Hälfte. u. 2. Hälfte. 1. Abtheilung' (Leipzig, 1850-52), containing an exposition, as complete as possible, of the minute structure of the organs and systems of man. With these are to be compared the yearly Reports of Henle, in Cannstatt's 'Jahresbericht,' and those of Reichert, in Müller's 'Archiv,' in the latter of which, more objective views and an earlier appearance would be desirable.

Useful figures are found in all the works above cited, with

[1] Translated for the Sydenham Society, 1847.

the exception of those of Bichat, Weber, and Bruns; furthermore, the figures of injections in Berres' 'Anatomie der Mikroskopischen Gebilde des menschlichen Körpers,' Heft 1-12 (Wien, 1836-42), are for the most part excellent, as are the representations of tissues in R. Wagner's 'Icones Physiologicæ,' second edition, by A. Ecker. Those of Langenbeck, 'Mikroskopisch-anatomische Abbildungen.' Lief. 1-4, (Gottingen, 1846-51); of A. H. Hassall, 'The Microscopic Anatomy of the Human Body' (London, 1846-49); and Mandl, 'Anatomie Microscopique' (Paris, 1838-48), are middling; while, on the other hand, those given by Quekett, 'Catalogue of the Histological Series in the Museum of the Royal College of Surgeons of England' (London, 1850), are admirable.

As regards Microscopes, I may express my opinion that of the more easily accessible, those of Plössl, Oberhäuser and Schiek, take the first rank. In Italy Amici, in England Ross, Powell and others, produce instruments quite equal to the above, but out of the question for Germany; among small, cheap, but not particularly useful instruments for students and physicians, for 115 to 150 francs, George Oberhäuser (Rue Dauphine, 19, Paris,) furnishes the best. The much-famed instruments of Nachet are good, but inferior to those of Oberhäuser; on the other hand, the small ones of Schiek for 40 thalers, and those of Plössl for 70 to 100 Fl., would be very serviceable if these artists were as productive as Oberhäuser. For the use of the microscope I refer to J. Vogel, 'Anleitung zum Gebrauche des Mikroskops' (Leipzig, 1841); H. von Mohl, 'Mikrographie' (Tübingen, 1846); Harting, 'Het Mikroskoop deszelfs gebruik, geschiedenis en tegenwoordige toestand' (Utrecht, 1848-50), 3 Theile; Purkinje, article 'Mikroskop,' in Wagner's 'Handwörterbuch der Physiologie,' Bd. 2, 1844; in which works, as well as in that of Quekett, 'A Practical Treatise on the Use of the Microscope' (London, 1848, translated by Hartmann, Weimar, 1850, [also Ed. 2, London, 1852)]; and Robin, 'Du Microscope et des Injections dans leurs applications à l'Anatomie et à la Pathologie' (Paris, 1848), the preparation of microscopical objects is in part very elaborately treated of.

A collection of microscopical preparations is indispensably necessary for a more exact study of Histology, especially

sections of bones and teeth and injections. Every one may with a little trouble, form a moderate collection for himself, hints towards which he will find in the paragraphs standing at the end of each section of the special part, as well as in the works just cited. Microscopical preparations may also be exchanged with or purchased of Hyrtl, in Vienna; Dr. Oschatz, in Berlin; Topping, Smith and Beck, Hett and others, in London; and also in Paris. The largest private and public collections of microscopical preparations exist in Vienna, with Hyrtl (injections); in Utrecht, with Harting and Schröder van der Kolk (injections, sections, muscles, nerves); in London, in the College of Surgeons (animal and vegetable tissues of all kinds); with Tomes (sections of bones and teeth); and with Carpenter (hard tissues of the lower animals).

THE

GENERAL ANATOMY OF THE TISSUES.

I.—OF THE ELEMENTARY PARTS.

§ 4.

If the solid and fluid constituents of the human body be examined with the aid of strong magnifying powers, it appears at once that the smallest parts which they exhibit to the naked eye, as granules, fibres, tubes, membranes, &c., are not the ultimate elements in respect of form, but on the contrary, that all, in conjunction with an universally distributed, fluid, semifluid or even solid, homogeneous, uniting substance, contain minute particles which differ in different organs but in the same organs have always a similar appearance. There are various kinds of these so-called *elementary parts, simple* and *compound*. The simplest are quite homogeneous, without any trace of their being composed of heterogeneous portions and are nearly allied to the inorganic forms, the crystalline granules and crystals, which also occur in the animal organism. Others already show that they have suffered a differentiation into an investment and determinate, though homogeneous contents: in others again, the contents present differences. The most important among all these forms, which may be comprehended under the general title of "*simple elementary parts*," are the cells, which not only form the starting-point of every animal and vegetable organism, but also, either as cells or after having undergone manifold metamorphoses, make up the body of the perfect animal, and in the simplest animal and vegetable formations (unicellular animals and plants), even enjoy an independent existence. Compared with cells, all other simple elementary parts have quite a subordinate

importance, so far as their direct participation in the formation of the tissues and organs is concerned; while, from their being almost all contained in the interior of cells and from their being concerned in many and most important ways in the vital processes of these cells, their importance in other respects is very great.

The simple elementary parts, which at first wholly comprise the commencing animal (or plant), often unite in the course of development in such a manner that they lose their independence and cease to exist as isolated elements. In this manner compound forms arise, each of which answers genetically to a whole series of simple ones and which may most fittingly be called the "*higher elementary parts.*" Such a coalescence has hitherto been observed with certainty only in cells, and from these most of the tubular and fibrous elements of the body are produced.

§ 5.

Formative and nutritive fluid—Interstitial substance or matrix.—While in plants the elementary parts in by far the majority of cases, unite directly with one another, in animals there is a very wide difference; a peculiar interstitial substance which combines them, and is ultimately derived from the blood, is always in a lower or more distant relation therewith. If this take a direct share in the formation of the elementary parts it is called "formative fluid," *Cytoblastema* (Schleiden), from κύτος, a vesicle, and βλάστημα, germ substance; if it be present for their maintenance, it is called "*nutritive fluid;*" if it have nothing to do with either the one or the other of these functions, it is called the matrix or *connecting substance.* The cytoblastema is usually quite fluid, as in the blood, in the chyle, in many glandular secretions, in the contents of glandular follicles and in many embryonic organs; more rarely, viscid and like mucus, as in the gelatinous cellular tissue of embryos (*vide infra*), still more rarely solid, as the blastema from which the villi of the chorion arise and grow. The "*nutritive fluid*" takes the place of the formative fluid in all perfect organs; and except when it is contained in special canals and cavities, as in bones, teeth and perhaps in some cellular organs, is present in so small a quantity that it cannot

be directly observed. A matrix lastly, is found in cartilages and bones as a solid, homogeneous, granular, or even fibrous substance connecting the cellular elements and for the most part arising from the blood, independently of them.

[The occurrence of a solid blastema, growing independently, in the villi of the chorion and of a solid matrix deposited directly out of the blood, demonstrates that all parts of the body are not, as Schwann was disposed to believe, without exception developed from cells or in dependence upon cells. A few more recent authors, as Reichert, Donders, and Virchow, also consider that the connective tissue, excepting its elastic element, is to be reckoned among those tissues which are not at all, or not wholly, derived from cells; but, as we shall see below, incorrectly. On the other hand, it is certain that in pathological formations such masses very frequently occur, fibrinous exudations becoming changed in great measure, without previous organisation, *i. e.* cell formation, into permanent tissues.][1]

A. SIMPLE ELEMENTARY PARTS.

I.—ELEMENTARY GRANULES, ELEMENTARY VESICLES, NUCLEI.

§ 6.

In almost all animal fluids, whether contained in canals, or inclosed in cells, as well as in many more solid tissues, there are found and often in immense quantities, roundish corpuscles of very small, hardly measurable dimensions. Henle has called them elementary granules, and has expressed the opinion that they are vesicular. This, however, is not always true, since it is demonstrable that many of these corpuscles possess no investment. Such is the case with the fatty particles which occur in many cells and glandular secretions, with the granules of

[[1] The Enamel and the Dentine of the teeth, and the so-called Cuticle of the hair, (see §§ on Hair and Teeth, and 'Quarterly Journal of Microscopical Science' for April, 1853,) must certainly be regarded as structures which are not derived directly from the metamorphosis of cells. We are inclined also to believe, that the opinion of Reichert, Donders and Virchow, as to the nature of the connective tissue, deserves much more attention than Professor Kölliker seems disposed to bestow on it. See §§ on Connective and Elastic Tissues, and General Appendix.—Eds.]

the black pigment of the eye and of other coloured cells, the granular precipitates of biliary colouring matter, of different salts in the kidneys and in the urine; lastly, the protein granules (albuminous granules) which are found free in certain portions of the grey substance of the central nervous system and of the retina. Among pathological but very common formations, we must enumerate here amorphous deposits, the colloid granules in the thyroid and elsewhere, and the *corpuscula amylacea* of the central nervous system, although these sometimes attain a very considerable size. All these granules want the properties observed in the higher elementary parts, such as endogenous growth, multiplication, assimilation, and excretion, and so far incline towards the purely inorganic forms—crystals; which are also found, though less commonly, in the organism, as for example in the spleen, in the lungs (black columns), in the ear, in the cells of the præputial glands of the rat, in the blood-corpuscles of the dog and of fishes, in the fat-cells of man, and in the cells of the chorion of the embryo of sheep.

Elementary vesicles also occur very frequently, and are for the most part allied, physiologically, with the elementary granules, since, once formed they do not increase, and neither multiply by division nor by endogenous development. The milk-globules may with tolerable certainty be arranged among these; at first included within the cells of the nascent milk, they are subsequently found free, in enormous numbers, in the perfect secretion and, as Henle first stated, consist of the fatty matter of the milk, with an investment of casein. The immeasurably small molecules of the chyle and of the blood, are also, according to H. Müller's investigation, fat globules with a protein envelope, and similar vesicles may be found in most other fluids containing fat and albumen in abundance. In fact, since the discovery of Ascherson (Müller's 'Archiv,' 1840, p. 49), that whenever fluid fat and fluid albumen are shaken together, the fat globules which are formed always become surrounded by an albuminous coat, it is more than probable that whenever, in the body, fat and albumen in the fluid condition come into contact, similar vesicles are produced.

A peculiar class of elementary vesicles is formed by the elements which occur in the yelk of certain animals. We are

best acquainted with them in the yelk of the hen's egg,[1] in whose proper yelk-substance and yelk-cavity the globules which have been so long known are all vesicular, but have not the nature of cells. The membranes of these yelk-vesicles are excessively delicate and consist of a protein compound; the contents are fluid albumen, and, in the globules of the yelk-cavity, there is usually a large parietal fat globule, while in the others there are many smaller and larger ones. The development of these vesicles proceeds, in all probability, from the fat globules as in other elementary vesicles, from which, however, they are distinguished by the fact that they distinctly possess the power of growth, during which their contents undergo metamorphosis, since in many the number of fat globules increases with age. Similar vesicles exist, also, in the yelk of fishes, crustacea and spiders, and here, as in birds, they have only a temporary importance, since they are not directly applied to the formation of the embryo, but only serve to nourish it.

Lastly, free nuclei occur in many localities, either temporarily, where cells are formed immediately round nuclei, as in the chyle, the blood-vascular glands, the Peyerian patches; or permanently, as proper elements of the tissue, in the wall of the thymus vesicles, in the rust-coloured layer of the cerebellum, and in the granular layer of the retina.[2]

[Von Wittich ('De Hymenogonia albuminis.' Regimontanii. 1850), has lately given some information upon the formation of the so-called *Aschersonian* vesicles. According to Wittich, whenever oil and albumen come in contact, a portion of the oil is saponified by uniting with the alkali of the layer of albumen in contact with it, and this layer being thus rendered insoluble by the deprivation of its alkali becomes precipitated, and thus forms the *Aschersonian* so-called haptogen membrane. According to this explanation the process would be purely

[[1] It is, however, by no means certain that the yelk-corpuscles of the hen's egg are elementary granules. According to Dr. H. Meckel (Die Bildung der für partielle Furchung bestimmten Eier der Vogel, &c., Siebold and Kölliker's 'Zeitschrift,' 1852), they are altered cells.—Eds.]

[[2] The blood corpuscles of man and the mammalia should be added to this list. See Wharton Jones, 'Phil. Transactions,' 1846.—Eds.]

chemical and not physical, and still less vital. In opposition to this view, however, Harting ('Ned. Lanc.' Sept. 1851), observed, not long ago, the formation of pseudo-cells by the agitation of albumen with mercury, in which case the albumen must be solidified, in the same way as by the mere shaking with water or otherwise, (Melsens, in 'Bull. de l'Acad. de Belgique,' 1850. Harting, &c.). Again, if by the bringing together of albumen and chloroform, serum-casein and fat, chondrin and chloroform,—albuminous, casein, and chondrin membranes are formed, as Panum observed (see in part, 'Archiv f. Path. Anatomie,' iv, 2), it can hardly be permissible to assume any chemical action.]

II.—OF THE CELLS.

§ 7.

The *cells, cellulæ,* called also elementary cells, or nucleated cells, are perfectly closed vesicles of 0·005—0·01‴ in mean diameter, in which we may distinguish a special investment, the *cell membrane,* and *contents.* The latter are always composed of a fluid, containing formed particles of various kinds, and a peculiar rounded body, the cell-nucleus, which again contains in its interior a fluid and a still smaller corpuscle, the nucleolus. These cells, which must be considered to be endowed with peculiar vital powers, and to be capable of absorption and assimilation, of growth and of multiplication, not only at the earliest period, entirely compose the body of the higher and that of most of the lower animals, but almost wholly generate the higher elementary parts of the fully-developed body. In fact, even in adult animals, we find in very many places that the elements are simply in the condition of cells, and that as such they take a more or less marked share in the performance of the organic functions.

Fig. 1.

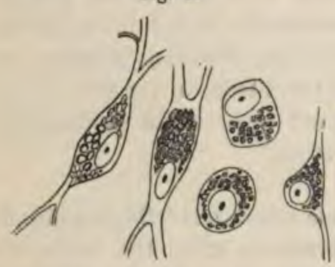


Fig. 1. Nerve-cells of the *Thalamus opticus* of man,—three of them having their processes torn off. × 350.

fluid are rare, (fat-cells, blood-cells, cells of the chorda dorsalis), and it is colourless or reddish; in general they contain, in addition, corpuscles in greater or less number, (elementary granules, elementary vesicles, perhaps crystals), and in fact, as a rule, young cells possess few, while older ones contain many, which are very often more densely grouped round the nucleus, or occupy only a single spot (coloured nerve-cells).

The *chemical* composition of the cells is as yet very obscure. The contents in most cells present certain generally disseminated substances, which occur dissolved in the nutritive fluid or cytoblastema, as water, albumen, fat, extractive matter, salts; a nitrogenous substance, which is precipitated by water and by dilute acids thus resembling mucus, is very extensively distributed and considerably impedes the microscopical analysis of the cells and tissues, inasmuch as it causes them to be obscure and granular, instead of clear and transparent. Many cells contain yet other compounds, as those of the liver, of the kidneys, of the blood, &c. The *cell membrane* consists of a nitrogenous substance, which is unquestionably a protein compound in young cells, as we may conclude from its solubility in acetic acid (partly even in the cold) and in dilute caustic alkalies. Subsequently the membrane in many cells, yet by no means in all, (*e. g.* not in the blood-corpuscles, in the deepest cells of the epidermis and epithelium, nor in the cells of the glandular follicles), becomes less soluble, and here and there more or less approximates the substance of the elastic tissue.

The *cell-nucleus* is a globular or lenticular, clear, or yellowish body, which in the mean measures 0·002—0·004‴, and rarely, as in the ganglion-globules and ova, attains a diameter of 0·01—0·04‴. All nuclei are vesicles, as Schwann supposed and as I have recognised to be their original and universal structure in embryos and adult animals. The membrane is very delicate in the smaller ones, appearing as a simple, fine, dark line; in the larger it is more marked, even of measurable thickness and limited by a double contour, as in the nuclei of the ganglion-globules, of ova and of many embryos. The contents of the nuclear vesicle consist, excepting the nucleolus, almost invariably of a pellucid or slightly

yellowish—never more darkly tinged—fluid, in which water and acetic acid precipitate the same dark granules as in the cells, for which reason the nuclei never preserve their natural homogeneous clear appearance, when examined according to the ordinary methods. More rarely the nuclei have formed contents, as the spermatic filament in the semen; in ova peculiar granules, the so-called germinal spots; also in the fat cells of *Piscicola* (Leydig). In respect of their chemical composition, only this much can be said of the nuclei, that their membranes are nitrogenous, and in general but little different from the substance forming the younger cell-membranes; they are, however, dissolved more slowly in alkalies, and are but slightly attacked by dilute acetic and mineral acids. In the latter circumstance they approximate the elastic tissue, from which, however, they are most essentially distinguished by their easy solubility in alkalies.

The nuclei are found, so far as I have observed, in all cells of embryos without exception, and in those of adults, so long as the cells are still young. In general only a single nucleus exists in each cell, except when it is multiplying; in the latter case, however, two or more nuclei arise, according to the number of the developing cells. In certain cells we meet with more numerous nuclei; thus, in those of the semen, 4, 10, 20, and more; also in the *substantia grisea centralis* of the spinal cord, of the supra-renal capsules, of the pituitary body, in the hepatic cells of embryos, in the fœtal medullary cells of bone, and elsewhere. That nuclei also occur free, and take part in the formation of certain tissues, has already been stated.

The *nucleoli* are round, sharply-defined, generally dark, fat-like granules, which, on the average, measure 0·001—0·0015‴, are often almost immeasurably small, and in embryos, in the germinal vesicles of ova as the germinal spots, and in the ganglion-globules attain the size of 0·003—0·01‴. In all probability they are always vesicular, as may be surmised from their sharply-circumscribed form, their similarity to elementary vesicles, and also from the circumstance that in certain cells, especially in ova and ganglion-globules, a larger or smaller cavity filled with fluid frequently becomes developed in them. The chemical composition of the nucleoli

is unknown, their external appearance, their similarity to the elementary vesicles, their disappearance in caustic alkalies, and their insolubility in acetic acid, would lead us to suppose them to be fat; the membranes may, as in the elementary vesicles, be a protein compound. Nucleoli are found in the great majority of nuclei, so long as these are still young, and in many during their whole existence; but nuclei also exist, in which nucleoli cannot be recognised with certainty, or at least become obvious only at a later period; and therefore, at present, the nucleolus cannot be so unconditionally recognised to be an essential constituent of the cell, as the nucleus. Generally, a nucleus contains only one nucleolus, frequently there are two, rarely three, and, in solitary cases, four or five may be present, which are then either eccentric or lie free in the nucleus.

[A short time since, Donders, in a very remarkable work (*vide infra*), expressed the opinion, that all cell-membranes consist of one and the same, or at least of very nearly allied substances, which agree in their characters with the elastic tissue. For my own part, I believe that all animal cell-membranes consist originally of the same substance—of a protein compound, in fact; that, however, in consequence of its subsequent metamorphoses, it may acquire differences of composition and of reaction. Many membranes in this manner become more resistant with time and, as Donders justly states, approach elastic tissue; others change into collagenous tissue, as those of the formative cells of the connective tissue, and of the cartilage cells during ossification; others into *syntonin*, as in the smooth muscles; into the so-called horn, and so on. If we assume the primitive cell-membrane to be a protein compound, and from the reaction of young cells and of embryonic parenchyma it can hardly be otherwise, we obtain a correspondence with the vegetable cell, since in this case the primordial utricle, consisting of a protein compound, can be considered as the analogue of the animal cell-membrane, whilst the cellulose membrane appears as a secondary product, as an excretion. Such may be the true condition also in those animal structures of the Tunicata which are formed of cellulose, in which case my assertion that here the cell-membranes are composed

of woody fibre, and that of Schacht (Müller's 'Archiv,' 1851), that they are nitrogenous, would coincide. If future investigation justify this comparison of the animal cell with the primordial utricle of plants, the further question would arise in animals, whether perhaps all the so-called metamorphoses of the cell-membrane are not to be laid to the account of *deposits which are thrown down upon the outer side of it*, similarly to the cellulose in plants, so that, perhaps, together with the original protein membrane, other secondary collagenous or elastic membranes, &c., might be distinguished, and even the most considerable thickenings of the animal cell be produced, in a manner analogous to that which occurs in the ligneous tissues of plants on the outer side of the protein membrane; so that, for example, within ossified cartilage-cells the original cell-membrane might perhaps still exist.

In all normal cells of the higher animals, the nuclei can be readily shown to be vesicles, and most beautifully so in embryos; only in those cells which arise directly round nuclei, are the nuclei at first more homogeneous, and subsequently exhibit a distinct membrane. In pathological formations, this character of the nucleus, which may be called an undeveloped form, is very frequent, and the nucleus-like structures in the Protozoa are also for the most part homogeneous bodies.]

§ 9.

Development of Cells.—With regard to the development of cells, we have to distinguish between their *free* origin and their production by the *intermediation of other cells*. In the former case the cells are developed, independently of others, in a plastic fluid, the cytoblastema of Schleiden, containing chiefly fat, protein, and salts in solution; in the other, or in cell-multiplication, the existent cells either produce the so-called daughter or secondary cells within themselves, or multiply by division; *endogenous cell-formation* and *fissiparous cell-formation*. Both kinds of cell-formation agree in this, that the cell-nuclei play a very important part, and appear to be the proper centres of development (bildungs-punkte) of the young cells.

§ 10.

Free cell-development is, in man and the higher animals, far less common than has been hitherto assumed, and under this category we can enumerate, so far as is at present known, only the development of the chyle and lymph corpuscles, of the cells of certain glandular secretions (spermatic cells, ova), and gland-like organs (closed follicles of the intestine, lymph glands, splenic corpuscles and pulp, thymus); lastly, of the cellular elements in the pregnant uterus, in the *corpus luteum*, in the medulla of fœtal bones, and in the soft ossifying blastemata. The separate steps of the process in this mode of cell-development have as yet been traced principally in the first-named cells, but much is yet wanting to complete our knowledge of it. This much is certain, that the origin of the cells is always preceded by the development of cell-nuclei, while it is doubtful, on the other hand, how these are formed. In the chyle and in the spleen we see as the first indication of cell-formation, rounded homogeneous-looking corpuscles of 0·001—·002‴, which, increasing somewhat in size, soon clearly appear to be vesicles, and often, upon the addition of water, exhibit in their interior, together with small granules, a large granule, like a nucleolus. Whether this last, as is certainly the case in the dependent mode of cell-development, arises before the nucleus and is the condition of the development of the latter, or whether it is formed subsequently therein; how, again, the nuclei themselves are developed, whether as originally homogeneous corpuscles, which subsequently exhibit a differentiation into inner and outer parts,—envelope and contents, or whether they are not, from the first, vesicular, cannot at present be decided.

Fig. 2.

The nuclei being once formed, the cell-membranes are developed around them, though not always in the same way. In the first place, they may be applied directly around the nucleus, so that the nascent cell is but little larger than its

Fig. 2. Contents of a Malpighian corpuscle of the ox, × 550: *a*, small; *b*, larger cells; *c*, free nuclei.

nucleus; or, in the second place, the latter may become surrounded by a greater or smaller quantity of solidifying cytoblastema, and it is only round this enveloping mass, which I have called an *investing globule*, that a membrane forms. This last occurrence in the free cell-formation has hitherto been observed only in the ovum, in which the germinal vesicle, *i. e.* the nucleus of the egg-cell, being first formed, surrounds itself with some yelk before the vitellary membrane appears. On the other hand, cell-development directly round the nucleus takes place in all the other localities which have been mentioned above, and is demonstrated by the occurrence, among free nuclei and large cells, of very small cells, which closely invest the nucleus or are but little separated from it. It may, however, be remarked, that perhaps in these cases also, the cell-membranes at their origin are separated from the nuclei by a very small quantity of cytoblastema, so small as to be incapable of detection.

[Free cell-formation is exceedingly frequent in pathological productions, and the cells in pus and in exudations of all kinds arise in this manner; in fact, all pathological cell-formation properly comes under this head. Usually the cell-membranes here arise directly round the nucleus, less commonly as it would seem round investing globules. With regard to physiological processes, as has been already shown, free cell-development has been much too readily taken for granted; and especially as regards the epithelial and horny tissues, as well as in many glandular secretions, it has been assumed without any sufficient grounds. Botany knows no free cell-development.][1]

[1] [There cannot be said to be any evidence of the occurrence of free cell-development in animals, so long as in any case cited it is not shown that the first-formed particles which make their appearance cannot have derived their origin from pre-existing formed particles, either by the detachment or fission of the latter. Not only does this condition remain unfulfilled for all the instances cited, but it has not been attempted, and would seem to be impossible. In pathological exudations, for instance, who shall determine that the first structural elements which appear, granules, free "nuclei," exudation corpuscles, &c., are not directly derived either from the blood, or from the tissue into which the exudation has taken place?—Eds.]

§ 11.

The development of cells within other cells, or their *endogenous origin*, is of very frequent occurrence, and easy to be observed in embryos. The commonest form of this cell genesis is, that a so-called *parent cell* produces *two secondary cells*, which *from the first wholly fill it*. The first thing to be observed in this case, in the parent cell, is a metamorphosis of its nucleus, which grows, acquires two nucleoli, becomes elongated, and divides into two. When this has once taken place, the nuclei become somewhat divaricated, and then a wall of separation arises between the cells, which divides the parent cell into two perfectly distinct spaces, each of which contains a single nucleus and one half of the contents. The mode in which the *multiplication of the nucleus* takes place, has not yet been made out with exactness. This much, however, is certain, that where clear observation is possible, it is always the nucleoli, which first divide into two and then diverge a little. In the nuclei, which have at the same time slightly elongated, there then usually appears, marking the first trace of their division, a median partition, which in favorable cases may be recognised as composed of two secondary nuclei applied to one another by their flat sides, and completely filling the parent nucleus. Very frequently we see, in the course of this process of multiplication of the nuclei, nothing more than, first an elongated nucleus, with a partition and two nucleoli, and then two hemispherical nuclei applied by their plane faces to one another, without its being possible to demonstrate with certainty any endogenous development of nuclei; so much the

Fig. 3.

Fig. 4.

Fig. 3. From the cephalic cartilage of an advanced tadpole. Parent cells, with 1 and 2 nuclei, or 2—4 secondary cells, and some interstitial substance, × 350.

Fig. 4. An elongated nucleus, and one containing two secondary nuclei, from the ovum of an *Ascaris dentata*, × 350.

less, as it is not to be doubted that, together with the latter process, a *multiplication of nuclei by division takes place,* in which an elongated parent nucleus, with two nucleoli, breaks up into two by the formation of a constriction which gradually deepens in the middle.

The further destiny of the parent cells, with a partition and two nuclei, is not always the same. As a rule, it appears that in each, two perfect secondary cells afterwards become evident, which may serve as a demonstration that the partition is double from the very first. At other times, distinct secondary cells are not recognisable, which however does not imply that there exists a mode of cell-development by the mere formation of partitions, but only that in such cases the secondary cells do not become distinctly separated from the parent cells. Whether the one process or the other take place, it rarely stops at one performance, but is generally repeated a certain, often very considerable number of times; in fact, as long as the organism grows. The parent cells either remain, or they cease earlier or later to be histologically distinct structures, and coalesce with the substance which unites the cells as a matrix. The occurrence of this endogenous cell-development, which may be called *cell-development around the collective contents,* and which agrees in all essential points with free cell-development around investing masses, has been made out with certainty in the young cartilage of all animals, and probably occurs in embryonic organs in general, in which, from the moment when they consist of actual cells, *the total growth essentially depends upon a self-multiplication of the cells* without free cell-development. Since, however, it is as yet undecided, whether perhaps cell-development by division, to which attention has been very lately drawn, does not play a part in the one case or in the other, our judgment, so far as regards the latter, must as yet be suspended, until more particular investigations have been undertaken; and the same holds good for many organs of the adult, as the horny tissues and certain glandular secretions. Only, when secondary cells are observed in parent cells, as especially in the pituitary body and in the supra-renal capsules, there can of course be no doubt as to the existence of endogenous cell-development.

Besides these most usual forms of cell-development, there exist yet a few others:

1. In the ova of most animals a peculiar process, the so-called cleavage of the yelk, occurs at the earliest period of development, which is to be regarded as the introduction to the formation of the first cells of the embryo; and since the ovum has the nature of a simple cell, it is a case of endogenous cell-development. This cleavage takes place as follows. After the original nucleus of the egg-cell, the germinal vesicle, has disappeared with the occurrence of fecundation, the granules of the yelk no longer form a compact mass as before, but become dispersed and fill the whole egg-cell. Then, as the earliest sign of commencing development, there arises in the midst of the yelk, around a new nucleolus, a new nucleus, the primary nucleus of the embryo, which operates as a centre of attraction upon the yelk and unites it again into a globular mass, the first "*cleavage mass*" (Furchungs-kugel). In the further course of development two new nuclei are formed by endogenous development from the first nucleus, and these, as soon as they have become freed by the solution of the parent nucleus, separate from one another for a short distance, act as new centres upon the yelk, and thus break up the first cleavage mass into two. In this way the multiplication of nuclei and of cleavage masses proceeds,—the former always taking the lead, until a very great number of small globules are produced, which fill the whole cavity of the yelk-cell; it is only in exceptional cases that the cleavage-masses break up after the development of three or four nuclei within them; so that then, instead of two, three or four cleavage-masses immediately proceed from one. This process is called *total* cleavage, because here the whole yelk is disposed around the newly-developed nuclei: *partial* cleavage is essentially similar, dif-

Fig. 5.

Fig. 5. The ova of *Ascaris nigrovenosa*,—1 from the second, 2 from the third, and 3 from the fifth stage of division, with 2, 4, and 16 division-masses: *a*, chorion; *b*, cleavage-masses. In 1 the nucleus of the lower mass contains two nucleoli, in 2 the lowest contains two nuclei.

fering only in the circumstance that it is not the whole yelk, but a greater or lesser portion, according to the animal, which invests the nascent nuclei.

When the process has attained a certain stage, the cleavage-masses all together, or in successive layers, surround themselves with membranes, and become actual cells, whence we are justified in considering this to be a process of endogenous cell-development. In fact, it is nothing else than an introduction to cell-development in the egg-cell, and differs from the ordinary phenomena of that class only in this, that firstly, the nucleus of the parent cell or the germinal vesicle, in most cases (Müller saw a division of it occur in the Molluscs which are developed within *Synapta digitata*[1]) has nothing to do with it; secondly, that the parent cell itself persists; and thirdly, that the investing globules developed by the successive multiplication of nuclei become cells only in the latest generations. This view is the more justifiable, as the cells which have arisen in consequence of the metamorphosis of the last cleavage-masses long continue to multiply by endogenous development; and the whole process of division may be regarded as a kind of endogenous cell-development, in which, on account of the rapidity with which the nuclei multiply, no formation of cell-membrane takes place in the early generations of "cleavage-masses."[2]

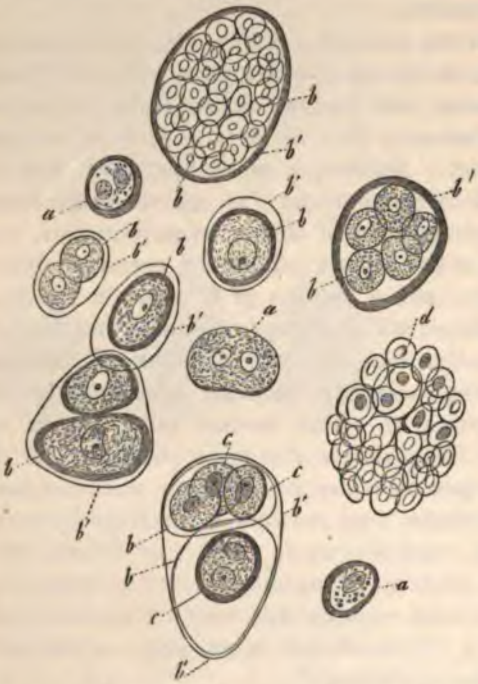
2. Closely allied, in some respects, to the cleavage process, are those forms of endogenous cell-development, in which a greater or smaller number of secondary cells are developed within *persistent* parent cells, as we see here and there in the cartilages, in the supra-renal capsules, and in the pituitary body. In this case there either arise in the ordinary manner, in a cell, two secondary cells, which wholly or partially fill it, and from these, by a continued multiplication, other generations,

[1] [Dr. Nelson (Phil. Trans., 1852, p. 580), has observed the same thing in *Ascaris mystax*.—Eds.]

[2] [We must altogether demur to the notion that the "nuclei" of the dividing yelk exercise any *attraction* upon the yelk substance. The careful observations of Reichert (Der Furchungs prozess und die sogenannte Zellenbildung um Inhaltsportionen, Müller's Archiv, 1846), of Remak (Ueber den Furchungs-prozess im Froschen-Eie, Müll. Archiv, 1851), and of Nelson, l. c., appear to furnish demonstrative evidence that no such attraction exists.—Eds.]

which sometimes lie quite free, and sometimes are wholly or partially included in the parent cells of the second generation; or a more free development of a secondary cell within a parent cell occurs, from which cell - development then takes place in one mode or in the other.

Fig. 6.



In connection with the process of endogenous cell-development, we may very properly speak of the formation of a great number of nuclei within cells, a process which is frequently the precursor of cell-development, but which may also continue alone. Even in the common endogenous cell-development (and also in the cleavage process) we not unfrequently observe three and four nuclei in a parent cell, so that then, instead of two secondary cells, many arise at once, *e. g.* in the hepatic cells of embryos. In certain animals (*Cucullanus, Ascaris dentata, Distoma, Cestoidea*), instead of cleavage-masses, nuclei alone are developed in the first stages of development, and it is only later, when by successive endogenous multiplication these have increased to a great bulk, that they become surrounded by

Fig. 6. Cartilage cells from a fibrous, velvety, articular cartilage of the condyle of the femur of man, × 350, all lying in a fibrous matrix, and readily isolated: *a*, simple cells, with or without a thickened wall, with 1 or 2 nuclei; *b*, secondary cells, or cells of the first generation, with 1 or 2 nuclei; 1, 2—5, or more, in parent cells; *b'*, *c*, cells of the second generation, 1—3 in number, in cells of the first; *d*, freed groups of secondary cells.

cell membranes. Something similar appears to take place in the cells of the germ in the Crustacea, in which 10—20 nuclei are often found (Rathke, 'De Anim. Crustac. gen.,' Regim. 1844). On the other hand, the numerous nuclei in the spermatic cells of most animals are, in general, in no way connected with cell-development, since the spermatic filaments are developed in them; and the like holds good of those cells of the lower animals, whose multitudinous nuclei are changed into thread-cells. The import of the number of nuclei in certain nerve-cells, and in the large cells of the bone-medulla, which Robin and I have observed, is doubtful; in the latter, I think it is not improbable that the multiplication of the nuclei is preliminary to their breaking up into smaller cells. In all these cases, it may be easily demonstrated that the nuclei multiply spontaneously, but it is generally doubtful whether this happens by division or by endogenous development.

Fig. 7.

[Cell-development round a mass of blastema containing a nucleus in its interior, which may take place either freely or in an endogenous manner (cell-development round portions of contents), had long ago been seen by von Siebold in the ova of *Distoma globiporum*, and by Bergmann in the cleavage-masses of *Rana*, but no further importance was attached to it. Vogt and Nägeli were the first who regarded this cell-development, as a deviation from the theory of Schleiden and Schwann, whereupon, supported by observations upon embryos, I (in 1844, 'Entwick. d. Cephalopoden') placed this as a second kind of cell-development, under the name of "cell-development round investing masses," beside that which takes place immediately round nuclei, and pointed out its very extensive occurrence, especially in embryos, where at first it is the sole mode. Later

Fig. 7. *a*. Peculiar granulated cells with many nuclei, from the youngest medullary cavities of the flat bones of the skull in man, × 350.

observations upon normal and pathological products have supported this view, and at the present time the formation of a cell-membrane immediately around the nucleus requires demonstration, rather than the opposite method. Endogenous cell-development occurs in many pathological products,—most frequently in cancer, yet the steps of the process have not yet been exactly made out. In plants this mode of multiplication of cells is the most extensive, and it occurs commonly as "cell development around portions of contents," more rarely (in the embryo sac) by free development within parent cells.][1]

§ 12.

A multiplication of cells by division certainly takes place in the red blood-corpuscles of the embryos of Birds and Mammalia, and in the first colourless blood-corpuscles of the Tadpole (Remak). It takes place also, in all probability, in the colourless blood-corpuscles of embryos, and in the chyle-corpuscles of adult Mammalia under certain circumstances. In all these cases, we see, in elongating cells, the production of two nuclei from the originally simple nucleus, apparently by division; the cells then suffer constriction in the middle, and contract more and more around the nuclei as they recede from each other, and at last separate into two cells, each of which contains a nucleus. In the chick we see blood-corpuscles in all conceivable stages of separation, so that at length they are connected only by a delicate thread, and there can here be no doubt whatever as to the actual occurrence of this process.

Fig. 8.

Fig. 8. Dividing blood-corpuscles of the chick, × 350.

1 [The endogenous development of secondary "nuclei" seems to us to be extremely doubtful, even upon the evidence adduced, and we have been unable to observe anything indicating that regularity of occurrence and importance of function attributed to the nucleolus by Professor Kölliker. In cartilage, in the tooth-pulp, in the homogeneous layers of the cutis, and in other localities in which unaltered "nuclei" occur, the presence and number of the granules which might be called nucleoli is in the highest degree variable and uncertain. The same irregularity as to the presence of nucleoli occurs in the plant (*vide* Von Mohl, l. c., and Schacht, 'Die Pflanzenzelle,' p. 30).

Upon this subject consult the valuable memoir of Remak ('Ueber extra-cellulare

Whether division ever take place in other cells than these is not yet determined. If it be allowable to explain, by this process of division, the occurrence of constricted cells with two nuclei, we may suppose it to take place in the nerve-cells, which, in young mammalia, are not unfrequently more or less divided or even united merely by a narrow isthmus, and also in the ciliated epithelium cells, which, although rarely, present two or three enlargements lying one behind the other, each with a nucleus. A peculiar kind of cell-development, which is very closely related to division, occurs in the formative cells of the ivory, which as they go on growing, multiply their nuclei and become constricted from time to time, so that whilst the portion next the ivory ossifies, the other serves in a manner as a reserve for the subsequent formation of fresh ossifying tissue.

Fig. 9.

[Schwann knew nothing of the occurrence of cell-division. The first who observed it in the blood-corpuscles of embryos was Remak ('Med. Verein.' 1841, No. 27; Schmidt, 'Jahrbücher,' 1841, p. 145; Canstatt, 'Jahresb.,' 1841), yet he subsequently retracted his opinion ('Diagn. und Pathol. Untersuchungen,' p. 100), and only now, since I have confirmed it and declared it to be true (Wiegm. 'Archiv,' Jahrg. 13, Bd. 1, p. 19), has he again advocated it ('Entwick. d. Wirbelthiere,' I). It is extremely probable that this mode of cell-development occurs very extensively, and it may perhaps turn out that in many embryos and adult tissues, in which a self-multiplication of the cells is certain, and yet in which no parent cells with secondary cells can be demonstrated, cell-development by division may occur instead of endogenous

Fig. 9. Dentine cells from the dog, × 350.

Enstehung Thierischen Zellen,' &c., Müll. Archiv, 1852), which by no means deserves the epithet of "no longer available;" in fact, Remak's views seem to be essentially correct.—Eds.]

cell-development. It is certain that the transverse and longitudinal division of the Protozoa is to be placed here, since these animals have the structure of simple cells, and the nucleus-like body they contain takes a share in the process of cell division, like that of the cell nucleus in common cells. In pathological formations cell-division has not yet been observed. In the vegetable kingdom it is rare, and has been seen only in the lower organisms; unless, indeed, we are to reckon here the constriction of the primordial utricle observed by von Mohl, in the course of endogenous cell-development.][1]

[1] [There can, we think, be little doubt that Von Mohl is quite correct in the view he takes of the multiplication of cells in plants by division, and therefore we are by no means inclined to agree with Professor Kölliker, as to the rarity of this form of cell-multiplication in the vegetable kingdom, nor, consequently, in what he says at the conclusion of the preceding note. All botanists of any note (Nägeli, Von Mohl, Hoffmeister, Alex. Braun, Schacht, Henfrey) maintain at the present time, that the process of cell-division so far from being "rare," is that which occurs in by far the great majority of cases in plants. "That the formation of cells, in all organs of plants (excepting the cells originating in the embryo sac), depends upon the division of older cells, is an opinion which could not for a long time past be opposed by any careful observer, unless he were misled by preconceived notions." (Von Mohl, Anatomy and Physiology of the Vegetable Cell,' 1851, Henfrey's translation). Nor can we agree with Professor Kölliker's estimate of the relative frequency of occurrence and importance of endogenous cell-development and cell-division in the animal world. In young cartilage, which is cited by our author as a locality in which endogenous cell-development takes place, we must affirm, on the contrary, that the process is as much one of cell-division as it is in any plant. At this period, the so-called "nuclei" of the cartilage completely fill their cavities (*e. g.* nasal cartilage of four-months' fœtus), and may be seen in all stages of division. The walls of the cavities grow in, *pari passu*, and eventually form a partition between the two nuclei, or rather primordial utricles, which have been thus developed from one.

Remak, who, in a very valuable paper (Ueber die Entstehung der Bindegewebes und Knorpels, Müll. Archiv, 1852), has advocated this view so far as cartilage and connective-tissue are concerned, does not appear to have seen the necessity of extending it to the other tissues. As Reichert, however, long since pointed out (see note, § on Connective Tissue), whatever determines the nature of the cartilage corpuscle and of its matrix, determines that of all the other tissues whose anatomical continuity with cartilage can be traced directly or indirectly. Thus a direct anatomical continuity may be shown to exist between the matrix of cartilage, the apparent fibrillæ of connective tissue, the fibrillæ of muscle, the homogeneous matrix of the cutis and of its papillæ, and the so-called walls of the epithelial cells; while a perfect identity in size, structure and relation, may be traced between the corpuscles of cartilage, the "nuclei" of connective tissue, those of muscle, of the papillæ and of the epithelial cells.—Eds.]

§ 13.

Theory of Cell-development.—Among the few hypotheses which have, up to the present time, been proposed in explanation of the development of cells, that of Schwann, who compares it with the formation of crystals, is certainly the most attractive. Without overlooking the differences between a crystal and a cell, which chiefly consist in the former being solid and homogeneous, in its growing by apposition, and in its being bounded by plane surfaces and angles, Schwann endeavours to explain cell-development as a crystallisation of organic matter, and to deduce from the permeability of the latter the differences in the phenomena presented by the two. In a fluid containing organic matters dissolved in considerable proportions, a granule, the *nucleolus*, is precipitated. Once formed, this attracts nutriment from the cytoblastema, and thus becomes the nucleus, which Schwann considers to be solid. This still goes on attracting to itself a substance, which, becoming more and more condensed, at last forms a membrane; which, allowing the passage of fluid cytoblastema through its pores, becomes detached from the nucleus, and we have a cell. In this exposition, we must admire not only the skilful, acute working out of the fundamental idea which the original treatise manifests, but also the assumption of a molecular attraction in cell-development, analogous to that which occurs in the formation of crystals, for the existence of which there is, in fact, decisive evidence (only in part, however, known to Schwann), such as the action of the nuclei in the cleavage process, in cell-division, in cell-development round portions of contents, in the cyclosis, and in the formation of granular precipitates in cells.[1] On the other hand, it is evidently going too far to call cell-development simply a crystallisation of permeable organic substances, since in this case important differences are overlooked, and non-essentials are made unduly prominent. For it must not be forgotten, that organic permeable substances also crystallise; that, in fact, if Reichert have observed correctly (Müller's 'Archiv,' 1849), and I see no reason for doubt, histogenetic substances capable of forming tissues, as albumen for instance, assume a crystalline form. Hence the molecular attraction

[1] [See note, p. 25.—Eds.]

concerned in the formation of cells is so far peculiar, that—1, it never produces geometrical solids, but even in the nucleus and nucleolus determines the globular form; 2, that it aggregates, not homogeneous but chemically different substances, as those which constitute the nucleus and the cell-membrane; 3, lastly, that without exception, in the development of the cell-membrane it limits itself, and does not, like the crystallising force, repeatedly apply layer upon layer. Of these differences, the two latter might perhaps be set aside, if with regard to the second point, it were assumed that the nuclei at first consist of the same substance as the cell-membranes, or are almost identical with them in chemical composition; or if we referred to the fact that in crystallisation also, different substances may unite into one crystal, or that a substance, *b*, may crystallise around a substance *a*.

In order to diminish the force of the third fact adduced (this objection, indeed, does not hold with regard to endogenous development, and therefore in almost all plants, since it is impossible here that the cells should produce any more layers around themselves), it might be urged that the permeability of the organic membranes, the exchange of constituents which takes place between the juices of the cell and the cytoblastema, and the application of the molecules attracted from the cytoblastema to the growth of the membrane, and to precipitates within the interior, are perhaps the reasons why the cells develope no new circumferential layers. It is not necessary to carry out this last possibility any further, nor to bring forward the difficulties which are opposed to this view also,—among which not the smallest is, that the organic development of vesicles does not stop at the formation of nuclei, but is only finished with the completion of the cell membrane; since in any case the facts brought forward are more than enough to demonstrate the insufficiency of Schwann's hypothesis. I do not see, however, anything better or more positive to substitute in its place, and I therefore think it will be most expedient simply to group together the ascertained facts into a few general propositions, which may, perhaps, be done as follows.

1. The nucleus of the cell arises in the first place, as a precipitate in an organisable fluid, and afterwards becomes consolidated in such a manner, that a special investment and

contents with a nucleolus appear. Its development may in this case be compared to that of inorganic precipitates, yet the constantly globular figure, and the size of nuclei which are just formed, indicate some essential though not yet recognised condition peculiar to them. Secondly, cell-nuclei are produced endogenously in nuclei, or by their division under the influence of a nucleolus, which also divides. Here is one condition which is never presented by crystals,—the division from an internal cause; while the other, the influence of the nucleoli upon the nucleus, can hardly be comprehended in any but a physical way, as a molecular attraction proceeding from the nucleoli, of an indefinable nature, which at last draws the entire half of the parent nucleus within its influence.

2. In the development of cells by division, the cell-nucleus plays exactly the same part which was previously ascribed to the nucleolus, and the occurrence of the formation of cells in this manner demonstrates that chemical conditions are not necessarily concerned therein.

3. In cell-development around portions of contents, and in the cleavage process, the nuclei also operate as simple centres of attraction (einfach attrahirend) upon a certain mass of blastema, and then follows the formation of a membrane upon the surface of this mass, which is most simply understood as a condensation of the blastema.

4. In cell-development directly around the nucleus, the investment with blastema is wanting, and the nucleus developes the membrane immediately around itself. This process admits of both a physical and a chemical explanation. In the first place, we may with Schwann assume that the nucleus attracts molecules, which, when they have reached a certain amount, condense into a membrane, and, by growing, become detached from the nucleus. Or secondly, it is conceivable, that the nucleus in some manner initiates chemical processes, which terminate with the formation of a membrane around it. In this way a coagulable substance might be produced within and excreted from it; or, like rennet upon casein, it might act upon the protein combinations in the cytoblastema, in such a manner that they should coagulate where in contact with it; or lastly, by the extraction of the alkali it might render an albuminous substance insoluble, as is the case in

the development of Ascherson's vesicles. Which of these various possibilities really obtains, must at present remain undetermined, yet, for my own part, I should prefer the first view, in order to retain one and the same condition, a physical one, for all the different modes of cell-development.

I do not think it necessary to enter at greater length, in the present place, into this very obscure subject, and I will therefore only once more express my opinion, that I hold the physical processes in cell-development, which may pass under the general name of molecular attraction, to be something quite different from those which attend crystallisation. Although in both, solids arise out of fluids, and grow by the further agglomeration of molecules, yet in cell-development *different* substances are as a rule superimposed, plane geometrical solids are never formed, and the process is always limited in the same way, after the formation of the cell-membrane. Since organic and even histogenetic substances are crystallisable, the reason of cell-development is not to be found in permeability nor in any of the other properties of organic compounds, which in fact, even if these substances did not crystallise, would not suffice to explain all the peculiarities of cells in question, nor their power of self-division and multiplication; but in those peculiar, as yet unknown combinations of the powers of nature which are concerned in organic development. To discover these is the further and difficult task of Histology, which to this end must be wholly directed to the so-called molecular forces of organic forms, especially to those *electrical phenomena* which must indubitably occur in the cells as well as in their derivative structures, the nerve-tubes and muscular fibres.[1]

[1] [The essential distinction between living organised matter (the cell) and mere inorganic formed matter (the crystal) appears to us to be here overlooked. If some inorganic substance should be discovered crystallising in the form of nucleated cells, it would not the more approximate to an animal or vegetable cell; for the essential character of the latter, *which is its passage through a definite succession of states and not its form merely*, would still be absent. It is this characteristic peculiarity of organised living beings, which has been exhibited with so much force by Alex. Braun, in the plant, under the somewhat fanciful title of 'Verjüngung' (rejuvenescence), but which equally obtains in the animal. The crystal tends to attain a permanent condition, the cell towards its own disappearance, either by death or division. The crystal tends towards an equilibrium with the forces around it, the cell incessantly disturbs that equilibrium,—life and change being one.—EDS.]

§ 14.

Vital phenomena of the perfect cells. Growth.—The cells, when once completed, perform a considerable number of functions, which relate as well to the form of the whole cell and of its contents, as to their chemical composition, and are called *growth* and *change of substance*.

As to *growth*, it occurs perhaps in all cells, though not in all to the same extent. It is clearly manifested in all those cells which are formed directly round a nucleus, since in this case the membranes which at first closely invest the nucleus, in time become more and more separated, whilst the cells which arise around portions of contents or investing masses, and are from the first provided with contents, often increase in size but very slightly. Growth is either in surface or in thickness. The former appears very usually to be *general*, when cells increase without altering their form, *e. g.* the ova, many nerve-cells, &c.; frequently however it is *partial*, as in all cells which depart from the primitive globular form, in such a manner that the cell-membranes only add new substance and extend at two or more points. Growth in thickness also occurs, to a certain extent, in all cells, since all cell-membranes become somewhat thicker with age; and it produces in some localities a very considerable thickening of the membrane, occasionally with evident lamination (as in the cartilage cells), and even gives rise to certain structures which have the greatest similarity to the sclerogenous cells of plants (bone-cells).

Fig. 10.

The nuclei and nucleoli also take part, to a certain extent, in the growth of the cells. In the former, a general growth is easily demonstrable in all growing cells; in many, as in those of the smooth muscles, of the epithelium of the vessels, of the formative cells of elastic tissue, and others, there is also a partial growth, in consequence of which they often assume the form of long slender rods. The *nucleoli* also not unfre-

Fig. 10. Cartilage cells of man, × 350. Two cells with thickened walls, from the cartilage of the great cornu of the hyoid bone, containing a clear drop of fat beside their nucleus.

quently grow with their cells, (nerve-cells, ova); but except when dividing they never assume any but the globular form.

Fig. 11.

Schwann has given an explanation of the growth, as well of the cell as of the nucleus. He considers that the molecules of the cell-membrane exert an attractive influence upon the fluid which surrounds them, and deposit its newly-formed particles among themselves; if the deposition take place between the molecules already present in the substance of the membrane, the cell becomes distended; if it take place only in the direction of the radius of the cell, the membrane becomes thickened. The nucleus grows less than the cell, because as soon as the latter is formed it no longer comes into direct contact with the concentrated cytoblastema. General growth takes place when the molecules of the membranes all attract equally; partial growth, when this happens only or especially at particular spots, where the apposition of new matter takes place to a greater extent. With reference to the mode of formation of precipitates and of crystals, this theory appears to me to explain very well the phenomena of general growth, supposing that we ascribe to the cell-membrane the faculty of readily taking up molecules and applying them to its increase. Such, however, must be the case, for the relations of the nuclei, which even when free, never grow very considerably, and *particularly never in one direction,*[1] show that the power of growth is not *simply innate in every organic membrane,* manifesting itself when sufficient formative material is offered, but requires peculiar conditions which are realised only in the cell-membrane. To account for partial growth, Schwann's view must be somewhat extended; for only those modes of growth in which the cells, during their increase in certain directions, lose nothing of their original dimensions in others, can be interpreted in

Fig. 11. Six developing bone-cells from a rickety bone as yet sharply defined from the interstitial substance:—*a*, simple bone-cells; *b*, a compound one, answering to a parent cell with two secondary cells; *c*, similar ones with three cells. × 350.

[1] [This is surely incorrect. The "nuclei" in the hair-pulp, in the tooth-pulp, in connective tissue, in organic muscle, grow in one direction to a very considerable extent.—Eds.]

Schwann's way, but not those in which the cells become narrower as they elongate; here we must assume that whilst new substance is deposited in the one direction, in the other an absorption takes place, for we can in nowise consider the process to be a mechanical one. For the rest, it may be remarked, that partial growth may depend upon the occurrence of assimilation, in particular cells, only in certain directions, as in the thickened vegetable cells with pore-canals, which is possibly connected with a one-sided direction of the currents in the cell-contents.

§ 15.

Processes in the interior of the Cells.—In order to obtain a clear conception of the processes which go on in the interior of cells, it would before all things be necessary to have a more exact acquaintance with the chemical composition of the cell-contents than we at present possess. Only two kinds of cells, the ovum and the blood-globule, have been investigated with care (*see* Remarks); but these have such peculiar relations that they can hardly be regarded as types of cells in general. However, we may from these analyses draw certain inferences with regard to other cells, and bearing in mind what micro-chemical investigation teaches us, it may be permissible to regard the cell contents in general, as a moderately concentrated solution of protein with alkaline and earthy salts, and dissolved or suspended fatty particles. From these common characters, presented without doubt by all cells, at least in their young condition, many cells differ very widely, insomuch as either some of these constituents greatly predominate or altogether new substances occur. Thus, there exist cells with much protein, as the nerve-cells; and with much fat, as the fat-cells, the cells of the sebaceous follicles, of the milk-glands, &c.;—then such as contain hæmatin, pigment, biliary and urinary constituents, mucus (epithelium cells), milk, sugar, &c. &c.

The phenomena manifested by these, so variously constituted cell-contents, during life, may be best enumerated as—absorption, assimilation, and excretion. These depend principally upon chemical and physical conditions, and are to a great extent capable of microscopic investigation, since very frequently the changes of form in the cell and the changes of its

contents go hand in hand. *Absorption* is manifested in all cells, but to far the greatest extent in those which at first have little or no contents save the nucleus. In these, the primary cause of the absorption is not to be sought in endosmose, but, as Schwann has indicated, in this—that while the membranes grow by the attraction of material from the surrounding fluid, by virtue of their porosity they allow substances to penetrate into the interior. This filling, however, does not take place by the cells admitting every kind of matter indiscriminately, but they exhibit peculiar relations to the cytoblastema, varying with the period and with the locality; so that they take up one constituent and reject another; and the like occurs with the absorptive powers of those cells which possess contents from their earliest existence.

That this is actually the case, is demonstrated, for instance, by the fact, that in embryos, notwithstanding the identity of the formative material in all cells, *i. e.* the plasma of the blood, some take up more of one substance, some more of another; and it is still more clearly evidenced by the fact, that the cell-contents of probably all cells are chemically different from the cytoblastema out of which they are formed and by which they are nourished, as has been clearly shown lately, in the ova and blood-corpuscles, which for example contain far more potass than the blood. The reason of this phenomenon may be generally stated to be, that the cell-membranes do not act as mere filters, but allow one substance or another to permeate them, according to their chemical composition, the constitution of the fluid which imbues them, their condition of aggregation, and their thickness.

Endosmose must also be taken into account as a condition in the absorptive actions of cells, though hitherto it has been too freely appealed to, and cells have been too often considered as vesicles provided with merely indifferent porous membranes. That endosmose operates is not to be denied, when it is observed how the addition of concentrated or diluted solutions, causes cells to dilate or to collapse, yet it is not easy to determine what influence such conditions have during life, nor what results are produced by the combined operation of the cell-membranes and their contents. From a few facts in vegetable physiology (growth of plants in arsenical and cupreous solu-

tions, without the admission of these substances), it might be believed that the membranes exercised the more important influence in determining absorption.

It is an important question, whether the substances received by the cells and composing them become modified by their vital processes. Schwann has answered it in the affirmative, and has denominated *metabolic* processes of cells, all those chemical metamorphoses which go on in them and in their separate parts; and justly so, for the occurrence of such chemical changes is not only very probable *à priori*, since in plants all such metamorphoses (and these of the most various kinds) take place in the cells, but may very easily be demonstrated by observation. These changes affect, firstly, the cell-membrane, and secondly the cell-contents. As regards the former, this much is certain, that the membranes of most cells not only become denser and more solid with age, but also that they take on a different chemical constitution, though it is impossible in particular cases to say on what the change depends. In the horny tissues, the membranes of the young cells are easily soluble in alkalies and acids, whilst subsequently they sometimes offer extreme resistance to their action: the same takes place in a few of the higher elementary parts, as the nervous tubules, the animal muscles, and the capillaries, in which the sarcolemma, the sheath of the nerve fibre, the capillary membranes, which are metamorphosed cell-membranes, react in a very different manner from the original formative cells. In the cartilage cells also, the membrane becomes more resistant with age, and in the course of ossification not only thickens, but is for the most part changed into collagenous tissue, which is subsequently impregnated with calcareous salts. These examples, which might be multiplied, may suffice to demonstrate the occurrence of a metamorphosis of the cell-membranes; further investigations will be needed to show upon what it depends, whether, as it would seem, the original animal cell-membrane actually alters in composition in course of time, or whether the change in the reaction depends upon the addition of foreign substances, on the incrustation of the membranes with salts, and so forth, such as botanists are inclined to assume for the vegetable cell-membranes, or whether it depends upon secondary deposits on the exterior of the original membranes.

The changes of the cell-contents are of two kinds, *formative* and *resolvent*. Both processes are easily followed in the embryos of different animals, in which, in the first place, the primary formative cells, which at the beginning are distended with the elements of the yelk, especially with oil, acquire by degrees more fluid and homogeneous contents, the yelk granules dissolving, sometimes from the cell-membrane towards the nucleus, sometimes from within outwards; and secondly, in cells thus formed, the most various new formations take place, among which that of hæmatin, of different kinds of pigment, and of fat, are the most obvious. But metamorphoses of the cell-contents are very common in adult animals also, and are at the same time very important, since in many places, on account of the great number of cells which are affected in the same way at the same time, unexpectedly great results are produced, as one of the most important of which we may name the biliary secretion, which is brought about, so to say, only by the activity of the many millions of cells which form the liver. A pretty series of changes may also be traced in the fat cells, which, according to the deficiency or superfluity of nutritive fluid, in the one case lose their proper contents, and may even become cells containing mere serum, in others are filled to bursting with drops of oil; again, in the cells of the fat-secreting glands, which at first contain but little fat, and finally become crammed with it; and also in the lymph-corpuscles, which develope the colouring matter of the blood within themselves, and thus become blood-corpuscles.[1] The formation of mucus, again, must probably be assigned to the epithelial cells of the mucous glands and mucous membranes; that of the so-called pepsin to the cells of the gastric glands; and that of semen to the spermatic cells. A multiplicity of confirmatory evidence is afforded by comparative anatomy, and I will here only advert to the development of the concretions of uric acid in the renal cells of the mollusca, that of sepia in the cells of the ink bag of the Cephalopod, of crystals and concretions of different kinds, in the cells of the invertebrata, and of certain pigments in those of the mollusca. Pathological anatomy affords us the pigment formations, the metamorphoses of cells containing blood-corpuscles and the fatty deposits in cells of all kinds.

[1] [In the oviparous vertebrata.—EDS.]

Manifold morphological phenomena go hand in hand with these changes, such as the thickenings of the cell-membrane, which have been already adverted to, with laminated depositions upon their inner surface, and even with the formation of pore-canals; as the precipitation in the cell-contents of granules of different sorts, as of pigment, albumen, casein (in the yelk, perhaps in the hepatic cells); and as the formation of fat drops, of elementary vesicles, of concretions, crystals, and nuclei. Even movements resembling the cyclosis of plants appear to occur in the cells of the lower animals (seen by me in the cells of the arms of a minute Medusa, a new *Æginopsis* from the Mediterranean, and of *Polyclinum stellatum*), and in Protozoa (currents in *Loxodes bursaria*, contractile vesicles in different genera); while, on the other hand, the Brownian molecular movements, *i. e.* a more or less active tremulous motion of granules without further change of place, which may be observed in many cells under the microscope, most beautifully in the pigment cells of the eye, are also, perhaps, hardly to be reckoned among vital phenomena.

The nuclei also occasionally, though upon the whole rarely, take part in the changes of the cells. The commonest of these appearances is their becoming clear, as a consequence of the liquefaction of the at first more viscid contents, upon which circumstance it depends that in young cells they are homogeneous, while in the larger they evidently appear to be vesicles. A formation of granules in the nuclei is very rare (see above); concretions, colouring matters, and crystals, are also not found here in animals; on the other hand, the development of the urticating threads in certain animals and that of the spermatozoa, takes place in nuclei.

In endeavouring to explain the metabolic processes of cells, we must in all cases especially regard the cell-nucleus; for just as it excites the development of the cell, so is it the centre of the currents of the contents, and of the deposits and solutions; but it is not to be regarded as the sole agent, for, firstly, it does not appear why the cell contents should not, like the cytoblastema, become changed of themselves; and, secondly, the changes of the cell-membrane are, at all events, more independent, and probably also have a certain influence upon the cell-contents, as the depositions which take place upon it,

and the solution of the solid contents which often occurs in its neighbourhood, demonstrate. To assume with Schwann a special metabolic force is incorrect, for, in the first place, the causes of the metabolic phenomena are certainly very various; and, secondly, there is every reason to reduce them to known molecular forces. Thus, for instance, even the action of the nucleus[1] may not unfittingly be compared with the so-called catalytic, or contact action, inasmuch as it is hardly at all altered during the changes of the cells, and consists of a nitrogenous substance, which like pepsin, (which is also nothing but cell-contents), very readily produces a chemical alteration in other substances. The relation of the cell-membrane to absorption also, may even now be referred to the general laws of imbibition and diffusion.

[I here give two analyses as examples of the chemical composition of the cell-contents. The yelk of the hen's egg contains: water, 48·55; casein, 13·93; albumen, mixed with casein, 0·892; albumen, 2·841; membranes of the yelk vesicles, 0·459; fats, 31·146 (30·46 according to Gobley), consisting of olein and margarin, 21·304; cholesterine, 0·438; lecithin (containing phosphoric acid), 8·426; and cerebrin; salts, 1·523; a hundred parts of the ash yielded, potass, 8·60—8·93; chloride of sodium, 9·12; phosphatic salts, 66·7—67·8; lime, 12·21; magnesia, 2·07; oxide of iron, 1·45; silica, 0·055. The blood-corpuscles contain: water, 68·88; hæmatin, 1·67; globulin and membranes, 28·22; fat, 0·23; extractive matters, 0·26; mineral substances (without iron), 0·81; of which, chlorine, 0·16; sulphuric acid, 0·006; phosphoric acid, 0·4; potassium, 0·33; sodium, 0·10; oxygen, 0·06; phosphate of lime, 0·01; phosphate of magnesia, 0·007. To these must also be added, free oxygen and carbonic acid, which likewise occur in the yelk.

We have here instances of cells containing much protein, and especially fat, and may consider them to be fair examples of this kind of cell. The comparison of the contents of these cells with the plasma of the blood, out of which those of the

[1] [This "*action of the nucleus*" is a wholly hypothetical though a very general assumption. It is important to bear in mind, on the contrary, that there is every reason to believe that the molecular and chemical changes of the cell-membrane and the nucleus are independent of one another.—EDS.]

one kind are formed, while the others live in it, is very interesting. In the blood-globules there is a considerable preponderance of solid constituents, since the blood-plasma only contains about 10 per cent. of solids, which is evidence[1] that there are cells whose contents do not attain an equilibrium with the cytoblastema by which they are supported. With regard to particular substances, the blood-corpuscles contain more fat; hæmatin, which is not found in the plasma; more potass and phosphoric acid; less chlorine, extractive matters, soda, and earths. The yelk of the hen's egg contains also considerably more solid constituents than the blood, which however is here less surprising than in the blood-corpuscles which swim in the blood-plasma. It is interesting, that the relative proportions of the different substances are quite different in this case from the other. We have, namely, an exceedingly large quantity of fat, more protein and salts; and among the latter, again, more potass, and also more earthy salts.

Even these facts indicate a considerable independence of action in the cells; but those which have been lately made known by Ludwig, tend still more forcibly in the same direction; for the influence of the nerves upon the salivary glands discovered by this observer must, I believe, be so interpreted, that it is not only the *membranæ propriæ* of the vesicles of the salivary glands, which are so altered in their molecular relations by the nervous influence that they directly exercise an energetic attraction upon the blood-plasma which surrounds them, but the epithelial cells which line them also. If this really be the case, we have an insight into an altogether new condition regulating the absorptive powers of cells, and at the same time cell-life is brought into such connection with the activity of the nervous system, that it no longer appears out of reason to speak of the positive functions of the latter. Such relations are in nowise opposed to analogy, since in the contractile elements we have already a connection between nervous activity and the modification of cell-contents, which perhaps upon further investigation may come under the same general category as the foregoing. In any case, these considerations lead anew to an exact investigation of the

[1] [This would be true only if the major part of the solid constituents of the blood-corpuscle were its contents; this, however, is not the case.—Eds.]

molecular forces of cells, especially of those electrical phenomena which will certainly be found in them.

[Very recently Donders (Nederlandsch. Lancet.) has justly brought forward a character which until now had received no attention, viz. the elasticity of the cell-membranes and the pressure consequently exercised upon the cell-contents. It is an ascertained fact that the cell-membranes are elastic; and it thence naturally follows that, according to the greater or less amount of the contents of the cells, so will these suffer a greater or a less pressure. This, however, reacts again upon the absorptive and excretive processes, so that under a more considerable pressure the latter, under a less, the former prevails, and in certain circumstances it may conduce to the maintaining of a regular interchange of substances. Donders believes, that the greater density of the cell-contents may be derived from their always being under greater pressure than the cytoblastema.]

§ 16.

Excretive processes.—The vegetative functions of animal cells are not limited to mere absorption and metamorphosis, but substances are excreted as a result of their operation. This may take place in two ways.

1. *The cells give out unaltered, the substances which they have received from without.*—This occurs in the epithelium cells of those glands which, like the kidneys, lachrymal glands, lungs, &c., simply permit of the discharge of substances from the blood, also in those cells which line the serous membranes, and probably many others.

2. *The cells excrete substances which they have prepared within themselves.*—Thus the blood-cells give up their hæmatin in dilute blood-plasma; the fat cells their fat in emaciated persons; the hepatic cells, bile; those of the gastric glands, gastric juice; those of the mucous glands and membranes, *mucus*.

The occurrence of these excretions, of which, in fact, there are assuredly very many with which we are still unacquainted, may in some cases be explained by exosmose; in others however, as in the secretions of the glands, this cannot take place. Here the exit of the contents is a consequence of the pressure

to which they are exposed, which pressure is to be referred upon the one hand to the force of the blood, on the other to an attractive force exercised by the cells themselves in absorbing the substances, and to the elasticity of the cell-membranes.

The excreted matters in general no longer continue in the organism, but are completely removed as in the glands; in a few localities they remain, taking a solid form, as extra-cellular substance, outside the cells, and form the genuine *membranæ propriæ* of the glands (*e. g.* of the renal canals), the proper envelope of the *chorda dorsalis,* and probably also the so-called vitreous membranes (capsule of the lens, *membrana Demoursii*). An intercellular substance is rare in animals, for the matrix of the cartilages and bones, which for the most part is not excreted by the cells, but is deposited from the blood-plasma or is even formed out of the cells, does not come under this head. It may be said to be present in a smaller quantity and more fluid, however, not only in the cellular tissues, but also in the higher structures, among which there everywhere exists a small quantity of connecting substance. Inter-cellular spaces developed by the excretions of cells between one another, have not been demonstrated with certainty in animals, yet it is probable that most glandular cavities and those of the heart and of the great vessels are of this nature, since they appear to arise by the excretion of fluid in the interior of originally compact masses of cells.

[My view, that the genuine *membranæ propriæ* and the vitreous membranes are formed as excretions, is founded particularly upon the examination of the *chorda dorsalis* and of the renal canals, in which it may be readily shown that the structureless membranes are secondary formations, arise in intimate union with the cells of this part, and from the very first appear perfectly homogeneous. The supposition of many authors, especially of Reichert, that these membranes belong to the homogeneous connective tissue, is readily refuted by chemical examination, since they yield no gelatine, but consist of a substance which most closely approximates to the sarcolemma and elastic tissue (comp. Mensonides in 'Nederl. Lancet.' d. iv, 694, and Donders, *ibid.,* August, 1851, p. 73). To what extent homogeneous membranes formed by excretions from

cells, occur among animals is not yet determined, but the homogeneous chitin-investments of the intestine, and of the external surface in the *Articulata*, appear to be of this nature.]

§ 17.

Contractility of the Cells.—Among the vital phenomena of cells must be enumerated those contractions which are manifested by cell-membranes and also by cell-contents. Contractile cell-membranes are possessed by many if not all Protozoa; and among subordinate cells, by the yelk-cells of the Planariæ, the heart-cells of many embryos (*Alytes, Sepia, Limax*), the cells of the tail of embryo *Botrylli*. The *cilia* also, as processes of the cell-membrane, may be mentioned here. Contractile cell-contents are found in the fibre-cells of the smooth muscles, in the stellate cells of the skin of the embryo of Limax, and in the animal muscular fibres; which last, as they consist of a number of united cells, may be here enumerated. Here also I place the contractile phenomena exhibited by the contents of the Protozoa (contractile vesicles) and by the Rhizopoda.[1]

[Donders has recently promulgated the view that it is only the cell-contents which are contractile, not the cell-membranes. Although it must be granted, that it is difficult, in the cases in question, to decide what part of the cell contracts, yet it seems very hazardous to endeavour to refer the movements of the cilia in plants and animals, in free and combined cells, to indemonstrable contents in these cilia communicating with the cell. In the cells of the Planariæ and in the Protozoa, any one who has actually seen the movements will hardly refer them to anything but the cell-membranes. In the transversely

[1] [To this list of contractile cells must be added the colourless corpuscle of the blood of man, the Frog and the Skate, and probably that of other Vertebrata (Wharton Jones, *l. c.*), the cells which lie in the meshes of the areolar tissue of the disc of the Medusæ (*Cyanæa*), and the young epithelium cells (mucus-corpuscles) of the mucous membranes, in which most distinct protean movements, like those of the colourless corpuscle, may be observed. It is certainly the membrane which contracts in these cases, for it pushes out processes which are only subsequently filled by the granular contents.

In the lower plants (*Algæ*) the occurrence of contractile processes in the shape of cilia is universal, and the contractility of the cell substance in the zoospores of *Volvox* is evinced by the occurrence of a rhythmically contracting space in them. (*See* Busk on *Volvox globator*, 'Quarterly Journ. of Micr. Sc.,' No. 2, 1853.)—Eds.]

striated muscular fibres on the other hand, it is evidently the fibrillæ or the contents which are contractile, and the sarcolemma, as an elastic yielding body, only moves with them: the same appears to hold good with the muscular fibre-cells, in which a special membrane cannot be demonstrated.]

§ 18.

Metamorphoses of Cells—Kinds of Cells.—The destination of the cells which are found at an early period in the organism is very various. A very considerable portion of them remain but for a short time in their primitive condition, and subsequently coalesce with others to form the higher elementary parts. Another portion, while they enter into no such combinations, change more or less their previous nature; as the horny plates of the epidermis and nails. Many cells, lastly, never become metamorphosed at all, but remain as cells, until sooner or later, often not before the decay of the organism, they disappear accidentally or typically, as the epithelia, glandular parenchymata, &c.

The permanent cells may be most conveniently arranged under the following heads:

1. *True cells,* which have in no essential respect altered their cellular nature. These occur in the epidermis (*stratum Malpighii*) and the epithelia; in the blood, chyle, lymph; in the glandular secretions, in the fatty tissue, in the grey nervous substance, the red bone-medulla; in the glands (liver, spleen, suprarenal capsules, closed glandular follicles), and the cartilages. According to their form, these cells may be divided into round, discoid, cylindrical, conical with cilia, and stellate; according to their contents, they may be distinguished as containing fat, protein or serum, hæmatin, bilin, pepsin, mucus, or pigment; and as to their modes of occurrence, some are either isolated in fluids or in solid tissues, others are united into a simple cellular parenchyma, while others are conjoined by an intercellular substance of one kind or another.

2. *Metamorphosed cells,* which have more or less altered their original structure. To these belong:

a. The horny scales: flattened, polygonal, or fusiform; their membrane being fused into one mass with the contents. In the epidermis, the laminated pavement epithelium, the hairs and nails.

b. The contractile fibre cells: fusiform, slightly flattened, considerably elongated cells, whose membrane, together with its soft, solid contents, is changed into a contractile substance. In the smooth muscles.

c. The tubules of the lens: very much elongated cells, with viscid, albuminous contents.

d. The prisms of the enamel: greatly elongated, prismatic, and strongly calcified cells.[1]

e. The bone cells: thickened cells with pore canals which have coalesced with the homogeneous matrix of the bones and anastomose by means of excavations in it.

f. The transversely striated muscular cells: large polygonal cells, whose contents have become metamorphosed into a transversely striated tissue, such as is found in the transversely striated muscular fibre. In the endocardium of ruminants.

B. HIGHER ELEMENTARY PARTS.

§ 19.

The higher elementary parts correspond, genetically, to a whole series of the simple ones, and it is the cells only, so far as we know, which possess the faculty of producing them. The manner in which this takes place varies. Either the cells while they coalesce retain their cellular nature, and to a certain extent their independence, in which case we have, according as they are fusiform or stellate cells, *cell-fibres* or *cell-reticulations;* or the cells in uniting totally surrender their independence, in which case they form, if they are arranged in lines, *elongated elementary parts;* or are united by many offsets,—*networks;* or are fused together upon all sides,—*membranes.* The two former of these again, according to the kind of modification undergone by the contents of the united cells, appear either as *fibres,* bundles of *fibrillæ* and *tubes,* or as *fibre-networks* and *tubular plexuses.* Since all these elementary parts will be spoken of at length afterwards, among the tissues, we may here simply enumerate them as follows. They are:

a. The cell-fibres and cell-networks.—To these belong a part of the nuclear fibres of authors, the cartilage cells of certain

[1] [*Vide infra,* § on the Teeth.—Eds.]

Plagiostome fishes (see Leydig, 'Beiträge zur mikr. Anat. u. Entwickel. d. Rochen u. Haie.,' Leipzig, 1852), the pigment cells of the *lamina fusca, pia mater,* and of Batrachian larvæ, the networks of the nerve cells in the brain of the Torpedo (R. Wagner), the fatty substance of the Lepidoptera (H. Meyer, 'Zeitschrift für wiss. Zool.,' Bd. i, st. 178).

b. The elastic fibres, fibrous networks, and fibres.

c. The fibres of connective tissue, the networks of connective tissue (reticulated connective tissue), *and the membranes composed of connective tissue* (homogeneous connective tissue).

d. The transversely striated muscular fibres and muscular-fibre networks.

e. The nerve-fibres and nerve-fibre networks.

f. The capillary plexuses of the blood-vessels and lymphatics.

g. The tracheæ and tracheal plexuses of the invertebrata.

All these higher elementary parts possess essentially the same properties as cells, especially growth in length and thickness, absorption, metamorphosis, and excretion, and to some extent contractility; together with other functions which may perhaps also be demonstrated in cells. Their growth is manifested by the fact, that all, without exception, are much shorter and narrower immediately after their formation than subsequently; their absorptive powers, by the dependence of their functions upon the circulation, by the phenomena of resorption in the lymphatics and blood-vascular capillaries, and by the above-mentioned growth, which can only take place by the reception of substances into their interior. A metamorphic and an excretive power must be assumed to exist in them; it is testified by the well-known peculiar products of decomposition of the muscles, and also by the continual transmission of blood-plasma through the walls of the capillaries. The muscular fibrils possess contractility, and the processes in the nerve-fibres, though very peculiar, and at present not to be defined more nearly, may nevertheless in some respects be compared to the functions of the nerve-cells.

[With regard to the tracheæ, which are placed here only for completeness' sake, I long since found that their terminations are formed by the coalescence of stellate cells into tubes, in which the original cell-contents either remain or become de-

veloped into a spiral fibre; and I published a concise notice of the fact in the year 1849 ('Zeitschrift für wiss. Zool.,' Bd. i, p. 215, Anmerkung), a view which has since been confirmed by H. Meyer (Ibid., Bd. i), and more recently by Leydig (Ibid., Bd. iii, Heft 4).

Literature of the Elementary parts.—In addition to Schwann's work quoted above, may be named: Kölliker, 'die Lehre von der thierischen Zelle,' in Schleiden u. Nägeli's 'Zeitschrift für wiss. Botanik.,' Heft ii, 1845; Remak, 'Ueber extracellulare Entstehung thierischen Zellen und die Vermehrung derselben durch Theilung u. über Entstehung des Bindegewebes u. d. Knorpel,' in Müller's 'Archiv,' 1852, i. (No longer available. Remak assumes quite confidently, what I only indicated, that animal cells have a primordial utricle, without giving any demonstration of the fact; he describes the multiplication of cells by division to be widely extended through embryonic tissues; finds (what others will not easily succeed in doing) two membranes in the later cleavage-masses, and wrongly, denies altogether the occurrence of free cell-development); also the treatise of Donders, cited below under the head of elastic tissue; and the embryological monographs of Reichert, Bischoff, Vogt, Remak, and myself. Inasmuch also, as the doctrine of the vegetable cell is important for zoologists, I call attention to Schleiden's first treatise ('Abhandlung über die Bildung d. Pflanzenzelle,' Müll. 'Arch.,' 1837); to his 'Elements of Botany;' to Nägeli's Essay 'Ueber die Pflanzenzelle,' in the 'Zeitschrift für wissenschaftlich. Botanik,' Heft ii; and to Mohl's Monograph upon this subject, in Wagner's 'Handwörterbuch' ('Mohl on the Vegetable Cell,' translated by A. Henfrey, London, 1852). [To these should be added the more recent works of Dr. H. Schacht, 'Die Pflanzenzelle, &c.,' Berlin, 1852; and of Alex. Braun, 'Ueber verjüngung,' Leipzig, 1851.—Eds.]

III.—OF THE TISSUES, ORGANS, AND SYSTEMS.

§ 20.

The elementary parts of both the simpler and the higher kinds, are not dispersed irregularly in the body, but are united according to determinate laws, into the so-called tissues and

organs. Under the first denomination comes every *constant arrangement of the elementary parts always recurring in similar modes in the same parts;* under that of an organ, on the other hand, *a certain sum of elementary parts having a definite form and function.* When several or many organs of a similar or different kind are united into a higher unity, this is called *a system.*

The tissues are of different kinds, according as structural elements of one kind only occur in them, or as various elements and even organs take part in their formation. We can thence distinguish simple and complex tissues, which, however, cannot be sharply separated from one another, and which may be most fittingly arranged in the following series:

(*a.*) *Simple tissues.*

1. Epidermic tissue.
2. Cartilaginous tissue.
3. Elastic tissue.
4. Connective tissue.

(*b.*) *Complex tissues.*

5. Osseous tissue.
6. Smooth muscular tissue.
7. Transversely striated muscular tissue.
8. Nervous tissue.
9. The tissue of the blood-vascular glands.
10. The tissue of the true glands.

The organs may be divided like the tissues, into simple and complex.

To the simple belong:

(*a.*) *Horny tissue,* as the epidermis, the epithelia, hairs, nails, and the lens, which consist solely and wholly of epithelial cells of one kind or another.

(*b.*) *The true cartilages* and *the elastic cartilages,* which in their interior, with few exceptions, consist only of cartilaginous tissue, though externally they possess a vascular and nervous coat, *the perichondrium.*

(*c.*) *The elastic ligaments,* consisting of elastic fibres, with some connective tissue, and containing only at the surface a few vessels and nerves.

(*d.*) *The tendons, ligaments, true fibrous membranes,* and *fibro-cartilages,* containing a preponderance of connective tissue,

intermixed with fine elastic fibres, and sometimes cartilage cells in small quantities, and almost entirely devoid of vessels and nerves.

Complex organs are:

(*e.*) *The smooth muscles* and *muscular membranes;* and—

(*f.*) *The transversely striated muscles* and *muscular membranes,* both of which, besides their contractile elements, are abundantly intermingled with connective tissue, nerves, and blood-vessels.

(*g.*) *The nerves, ganglia,* and *higher central organs of the nervous system,* contain besides grey and white nervous substance, many blood-vessels, and special fibrous investments.

(*h.*) *The vessels* are composed of connective and elastic tissue, muscles and epithelium in various proportions, and are provided with vessels and nerves, only in their outermost layers.

(*i.*) *The bones and teeth,* which, together with their characteristic tissues, have peculiar soft structures, containing many vessels and nerves, and the former medulla also.

(*k.*) *The blood-vascular glands,* composed of a peculiar glandular element, in the form of closed follicles of different kinds, and many blood-vessels; with nerves also, and with abundant but generally non-contractile fibrous tissue.

(*l.*) *The true glands;* glandular follicles, vesicles or tubes with many vessels, nerves, and investing fibrous tissue.

(*m.*) *The vascular membranes,* as the skin, the mucous, serous, and proper vascular membranes, which in a matrix composed of connective and elastic tissue, generally contain very numerous blood-vessels and lymphatics, in part also simple glands and nerves, and are invested by special epithelial layers.

(*n.*) The separate organs of the *tractus intestinalis,* as the tongue, the oral cavity, the pharynx, the œsophagus, the stomach, and so forth, into the constitution of which, mucous, muscular and serous membranes, grouped in various ways, enter.

(*o.*) The higher organs of sense, into which almost all the tissues and many more simple organs enter.

Lastly, *the organs* enter into the formation of peculiar systems, of which we may distinguish the following:

1. *The external cutaneous system,* consisting of the corium, the epidermis, the horny tissues, and the larger (lacteal gland) and smaller glands of the skin.

2. *The osseous system,* consisting of the bones, cartilages, ligaments, and articular capsules.

3. *The muscular system,* consisting of the muscles of the trunk and of the extremities, the tendons, fasciæ, tendinous ligaments, and *bursæ mucosæ.*

4. *The nervous system,* composed of the larger and smaller central organs, the nerves and the higher organs of sense.

5. *The vascular system,* consisting of the heart, the blood- and lymph-vessels, and the lymphatic glands.

6. *The intestinal system,* composed of the intestinal canal, the organs of respiration, with the thymus and thyroid, the salivary glands, the liver, and the spleen.

7. *The urinary and sexual systems.*

As the separate organs and systems are particularly considered in the special part of this work, it is not necessary to speak at greater length of them here, and it is only requisite to define the tissues somewhat more closely—taking occasion at the same time to refer to some generalities concerning the organs.

§ 21.

Epidermic Tissue.—The morphological character of the epidermis is, that it is wholly constituted by independent cells intimately united together without any visible matrix, which are generally nucleated and in part are true vesicles, while in part they are metamorphosed into solid scales. In its chemical characters this tissue is but little known, though this much has been made out, that its cells contain chiefly an albuminous substance, in part also mucous; and at first all possess easily soluble protein membranes, which however, subsequently, become partially changed into a substance which more or less resists acids and alkalies,—the so-called *horn.* The physiological import of the epidermic tissue is to serve as a defensive covering to those parts of the organism which abound in vessels and nerves, and by the activity of its elements to take part in secretion and absorption. All epidermic tissues are non-vascular, and support themselves from a plasma which is yielded

by the deeper-seated vessels. They are very easily regenerated when their superficial portions are removed, and in this case they grow chiefly by the development of new elements in the deeper layers; even when wholly lost they are readily reproduced.

The epidermic tissue takes the following forms:

1. *Corneous tissue.*—This always consists of compact masses of cells, which are soft in the neighbourhood of their vascular basis, but at a greater distance become more or less solid and hard (corneous), and frequently lose their originally vesicular constitution and nucleus, and become the so-called horny scales. The following organs are formed by this tissue:

a. The Epidermis; which invests the exterior of the body, and is continuous at the great apertures of the internal cavities with the epithelium. It consists of two tolerably distinct layers; the mucous layer (*rete mucosum*), with soft, rounded polygonal cells, which, under certain circumstances, contain colouring matter. This layer applies itself accurately to all the inequalities of the corium (which nourishes the epidermis), and externally passes into the polygonal scales of the horny layer.

Fig. 12.

b. The Nails.—These may be regarded as a modification of the epidermis, whose horny layer has attained a still greater density; and, with its *rete mucosum,* lies upon a special depressed surface of the cutis,—the bed of the nail; and is partly sunk in a peculiar cleft,—the fold of the nail.

c. The Hairs.—Filiform epidermic[1] structures, seated upon a vascular papilla, in a peculiar sac, the hair sac, which is a process of the corium, and is lined by a continuation of the epidermis. The structural elements in the region of the papilla are soft and vesicular; the more distant are metamorphosed into three kinds of cells—plates, flat fibres, and more or less rounded irregular cells.

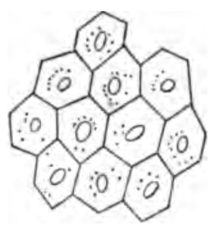
Fig. 12. Plates of the horny layer in man, × 350: 1, without addition, viewed from the surface, one with, a nucleus; 2, from the side.

[1] [It is to be questioned if the hairs are] truly epidermic structures, *vide infra,* § Hair.—Eds.]

2. *Epithelium.*—Soft nucleated cells, nowhere densely corneous; rounded, polygonal, fusiform, cylindrical or conical in shape; sometimes possessing cilia, sometimes not, and occurring in one or many layers. Hence we have the following forms:

a. Epithelium in a single stratum.

Fig. 13.



(1) *With rounded, polygonal cells* (pavement epithelium in a single layer).

This exists as an investment of the true serous membranes, of most synovial membranes, of the cerebral ventricles (*ependyma*) of the membrane of Demours, of the back of the iris, and of the inner surface of the choroid (pigment layer), of the capsule of the lens and of the *retina,* of the internal ear, of the *endocardium,* of the veins, of many glandular vesicles and canals (racemose glands, kidneys, sudoriparous and ceruminous glands, lungs), and of the *ductus interlobulares* of the liver.

Fig. 14.

(2) *With fusiform, superficially united cells* (fusiform epithelium).

Epithelium of the arteries, and of many veins.

(3) *With cylindrical cells* (cylinder-epithelium).

In the intestine from the cardia to the anus, in Lieberkühn's glands, in the excretory ducts of the gastric glands, as well as of all the other glands which open into the intestine; also of the lacteal and lachrymal glands; in the male urethra, the *vas deferens,* the *vesiculæ seminales,* the excretory ducts of the prostate, of Cowper's,

Fig. 15.

Fig. 13. Epidermis of a two months' human embryo, still soft, like epithelium, × 350.

Fig. 14. Epithelial cells of the vessels, the longer ones from the arteries, the shorter from the veins.

Fig. 15. Epithelium of the intestinal villi of the rabbit, × 300.

Fig. 16.

Bartholini's, and the uterine glands.

(4) *With cylindrical or conical ciliated cells* (simple, ciliated cylinder-epithelium).

Epithelium of the finest bronchiæ, of the nasal cavities, of the inner surface of the *membrana tympani*, of the Eustachian tube, of the uterus, from the middle of the cervix, up the Fallopian tubes, as far as the outer surface of the *fimbriæ*.

(5) *With rounded ciliated cells* (simple, ciliated pavement-epithelium).

Epithelium of the cerebral cavities of embryos.

b. Epithelium in many layers—

(1) *With cylindrical or rounded cells below, rounded, polygonal, more or less flattened cells above* (laminated pavement-epithelium).

Fig. 17.

Epithelium of the oral cavity, of the lower half of the pharynx, of the œsophagus, of the lachrymal canals, of the conjunctiva, of the tympanic cavity, of the vagina and female urethra, of the urinary bladder, of the ureters and pelves of the kidneys, and of certain synovial membranes.

(2) *With rounded cells below, more elongated ones in the middle, and ciliated conical ones above* (laminated ciliary epithelium.)

Epithelium of the larynx, trachea, and larger bronchiæ; of the nasal cavity, with exception of the *regio olfactoria;* of the lachrymal sac and duct; of the upper half of the pharynx.

Fig. 16. Ciliated cells from the finer bronchiæ, × 350.

Fig. 17. A simple papilla with manifold vessels and epithelium, from the gums of a child, × 250.

Fig. 18.

Among the epidermic tissues we may also enumerate the crystalline lens and the enamel.[1] The former consists of long tubular cells filled with albumen, which, as the study of development teaches, are formed by the metamorphosis of a part of the epidermis. The latter contains prismatic, densely-ossified long fibres, which, in all probability, are also nothing more than excessively elongated epithelial cells of the enamel organ of the embryonic tooth sac.

[The epidermic tissue is found through almost the whole animal kingdom, and as regards its elements, it exhibits no very considerable deviations in animals. One of its kinds, the *horny tissue,* appears to occur more generally, and to some extent in peculiar forms. To it belong (*a*), among structures which appertain to the skin: claws, hoofs, horns, spines, plates, and discs, bristles, feathers, and penis-spines. (*b*), Among appendages of the mucous membranes: the horny sheaths of the beaks of birds, of *Chelonia,* of the *Siren* and *Ornithorhynchus*; the horny teeth of the Cyclostome fishes; of the *Ornithorhynchus,* of the gill rays of fishes, and of Batrachian larvæ; the *whale bone,* the spines and plates of the tongue of Birds, *Mammalia,* and some *Amphibia*; the spines of the œsophagus of *Chelonia*; the jaws of *Cephalopoda* and other Invertebrata; the gastric teeth of many mollusks; the horny plates of the bird's stomach. In all these structures, but often only by the aid of caustic alkalies, horny plates of one kind or another, as in the corneous structures of man, are discoverable. On the other hand, the hard tissues of the Articulata differ not only morphologically but also chemically from them, consisting as they do of a peculiar substance, *chitin,* and exhibiting no cellular structure.]

Fig. 18. Ciliated epithelium from the trachea of a man, × 350: *a*. outermost part of the elastic longitudinal fibres; *b*, homogeneous outermost layer of the mucous membranes; *c*, deepest round cells; *d*, median long cells; *e*, outermost ciliated cells.

1 [*Vide infra,* note § on the Teeth.]

Literature.—Purkinje et Valentin, 'De phænomeno generali et fundamentali motus vibratorii continui,' Vratisl. 1835, (Discovery of ciliary movement in the higher animals); Henle, 'Symbolæ ad anatom. vill. int.,' Berol. 1837; 'On the distribution of the epithelium in the human body,' Berlin, 1838; and upon the development of mucus and pus, and their relation to the epidermis (first exact description of the different epidermic cells); Valentin, art. Ciliary Motion, in Wagner's 'Handwörterbuch;' Jäsche, 'De telis epithelialibus in specie et de iis vasorum in genere,' Dorp. 1847.

§ 22.

Cartilage.—Cartilage consists of a solid, but elastic, bluish, milk-white or yellowish substance, which presents two morphological conditions; appearing, firstly, as *a simple parenchyma composed of cells;* and secondly, as a *cellular tissue, with an intermediate substance or matrix between the elements.* The cartilage cells present little peculiarity in respect of form; they are generally round or elongated, frequently flattened or fusiform, very rarely stellate (in Cuttle-fishes and Sharks, and in *enchondroma*). Their membrane is ordinarily thick, frequently invested by concentric laminæ; the contents are clear and more fluid with a single nucleus, and, though not constantly, with one or many fat globules. The interstitial substance is either homogeneous or finely granulated or fibrous, even with clear separable fibres. The chemical characters of cartilage are in some respects but little known. It is ascertained, however, that the cells and the intermediate substance are composed of different substances. The membranes of the cartilage cells, in fact, are not dissolved by boiling, and offer a lengthened resistance to alkalies and acids, peculiarities which distinguish them from the substances which yield gelatine, but approximate them to elastic tissue. The contents of the cells coagulate in water and dilute acids, and are readily dissolved by alkalies. The interstitial substance is, in most cartilages, *chondrin,* and only in the reticulated cartilages is it a substance closely allied to that of the elastic tissue. Consequently the cartilages, which consist only of cartilage-cells, yield no gelatine upon boiling, and its occurrence is no essential character of cartilage. Physiologically, the solidity and elasticity of the cartilages are

particularly to be noted, as by these properties it is fitted for its various uses. In growing cartilages the change of material is very energetic; they constantly contain, in certain localities, numerous blood-vessels in peculiar canals; and, as I have demonstrated in the nasal cartilage of the calf, even nerves. Their growth takes place, firstly, by endogenous multiplication of cells, traces of which are always clearly to be observed in perfect cartilages; and secondly, by the deposition between the cells, which originally exist alone in all cartilages, of an interstitial substance from the blood plasma, which, according to Schwann, at first yields no chondrin even in the true cartilages, and subsequently gradually increases in quantity. In perfect cartilages the nutrition is by no means energetic; and it has, apart from the vessels of the perichondrium which invests many cartilages, and those of the neighbouring bone, no particular agent, except in the cartilages (septum of the nose) of a few mammalia, and in the plagiostome fishes, in some of which last, according to Leydig, even in old individuals, vascular canals exist (*Raja*), in others anastomosing, fusiform, or stellate corpuscles (Sharks). With age, the intermediate substance of certain true cartilages readily becomes fibrous, and very similar in its chemical characters to that of the reticulated cartilages, which demonstrates that these two kinds of cartilage are not widely separated; the true cartilages also not uncommonly ossify, vessels, cartilage, and medulla being formed in them at the same time. Cartilage possesses no power of regeneration, nor do wounds in cartilage unite by cartilage; on the other hand, an adventitious development of cartilage is not uncommon.

The different kinds of cartilage are:

a. Cartilage without interstitial substance, or parenchymatous cartilage. To this belong the *chorda dorsalis* of the embryo and of many adult fish; many fœtal cartilages; the cartilages of the gill laminæ of fishes in part; and those of the external ear of many mammalia.

b. Cartilage with interstitial substance.

Fig. 19.

Fig. 19. Portion of the chorda dorsalis of an embryo sheep, 6‴ long: *a*, sheath; *b*, cells, with clear vesicular spaces.

1. With a more homogeneous, chondrin-yielding substance: true cartilage, hyaline cartilage: it is found in the larger cartilages of the respiratory organs, those of the articulations, of the ribs, and of the nose; also in all *symphyses* and *synchondroses* immediately in contact with the bones; in the *talus ossis cuboidei*, and in the so-called ossifying cartilages of the fœtus.

Fig. 20.

Fig. 21.

2. With a fibrous interstitial substance, yielding no chondrin, or but very little: reticulated cartilage, yellow cartilage, fibro-cartilage in part; epiglottis, *cartilagines Santorinianæ, Wrisbergianæ*, cartilage of the ear and of the Eustachian tube; *ligamenta intervertebralia* in part.

[In the Invertebrata many tissues of a similar consistence to cartilage are found, but true cartilage has hitherto been discovered only in the Cuttle-fishes.]

Literature.—Meckauer, 'De penitiori cartilaginum structurâ Diss.,' Vratisl., 1836; J. Müller, in 'Poggendorf's Annalen,' 1836, p. 293; Rathke, in Froriep's 'Notizen,' 1847, p. 306; A. Bergmann, 'De cartilaginibus Disq. micr.,' Mitaviæ, 1850.

§ 23.

Elastic Tissue.—The elements of elastic tissue are cylindrical or band-like fibres, with dark contours, which vary in their

Fig. 20. Cartilage cells from the white layer of the cricoid cartilage, × 350. From man.

Fig. 21. Portion of a human epiglottis, × 350.

Fig. 22.

diameter from immeasurable fineness up to a thickness of 0·003‴, and even 0·005‴ (in animals even to as much as 0·008‴), and when they are present in quantity, exhibit a yellowish colour. These so-called elastic fibres are, when perfectly formed, quite solid, but may subsequently acquire little cavities in particular spots; and these, in one animal, the Giraffe (Quekett, 'Histological Catalogue,' i), are so regular, that the fibres present a pretty transversely striated appearance. The margins of the elastic fibres are in general quite rectilinear, but in some rare cases appear to be notched and even, as Virchow saw them, in newly-developed tissues, beset with a great number of shorter and longer pointed processes. Hitherto the *elastic fibres* have been separated from the *nucleus fibres*: since, however, the latter are distinguished from the former in nothing but their diameter; furthermore, as all elastic fibres are originally as fine as nucleus-fibres; and since, finally, the latter are not formed of nuclei alone, it will be better wholly to suppress the name of *nucleus-fibres*, and to divide the elastic fibres simply into *finer* and *coarser*. The elastic fibres are found either isolated as longer or shorter fibres, which may be straight or wind spirally round other parts (bundles of connective tissue, nerves), and in this case they are commonly of the finer kind; or by the anastomosis of fibres of different sizes, a so-called *fibrous elastic network* is formed, which is sometimes expanded in a membranous form, and sometimes penetrates other tissues to various depths. A modification of this fibrous elastic network is formed by the elastic membranes, in which the fibres are so closely interwoven, that a connected membrane arises, which in the most extreme cases no longer exhibits any indication of its previous nature, and appears as a perfectly homogeneous membrane with smaller gaps (the fenestrated membrane of Henle).

Chemically, elastic tissue presents very decided reactions, but the composition of its substance is not yet exactly known. In cold concentrated acetic acid, the elastic fibres, except that

Fig. 22. Elastic network from the *tunica media* of the pulmonary artery of a horse, with lacunæ in the fibre, × 350.

they swell a little, are not affected; if boiled for a whole day, however, they are gradually dissolved: nitric acid colours them yellow; Millon's test for protein tinges them red; whilst sulphuric acid and sugar have no action (red coloration) upon

Fig. 23.

Fig. 24.

Fig. 25.

them. In a moderately diluted solution of potass, elastic tissue remains, for a long time, unaltered in the cold, except that it swells up and becomes somewhat paler. Heated for a day with it, it becomes converted into a gelatinous mass. In water this tissue does not alter, even after sixty hours' boiling, but changes by boiling for thirty hours in Papin's digester into a brownish substance, smelling like glue, but not gelatinizing, which is precipitated by tannic acid, tincture of iodine, and corrosive sublimate, but not by the other tests for *chondrin*.

Fig. 23. Two secondary bundles of connective tissue from the arachnoid of man, with coiled and straight (interstitial) fine elastic fibres, × 350, and acetic acid added.

Fig. 24. Network of fine elastic fibre from the peritoneum of a child, × 350.

Fig. 25. Elastic membrane from the tunica media of the carotid of the horse, × 350.

Physiologically, the prominent characteristic of this tissue is its elasticity, in consequence of which it forms a most essential support to the motor organs, and also plays an important part in other situations, *e. g.* in the vocal ligaments. With respect to its development, the supposition of Schwann, that this tissue proceeds from cells, receives increasing support from modern investigations; in fact, in all those organs which subsequently contain elastic tissue, there may be discovered in embryos, peculiar fusiform or stellate, sharply-pointed cells, which by their coalescence produce long fibres or reticulations, in which at first, those localities where the bodies of the cells previously existed may still be recognised as enlargements containing elongated nuclei in their interior. In this condition the fibres not unfrequently remain, and they then form a modification of what were formerly called *nucleus-fibres*, or every trace of their previous composition disappears, so that quite homogeneous fibres or fibrous reticulations are produced. These may then either remain through life as fine elastic fibres and networks, or by increasing in thickness they may pass into the coarser form of the tissue. The more homogeneous elastic membranes are nothing but close elastic networks, whose fibres have so much increased in diameter, that only narrow spaces remain between them. The perfect elastic tissue appears to undergo very little change of substance—at least it is, so to speak, non-vascular, even when it occurs in large masses; on

Fig. 26.

Fig. 27.

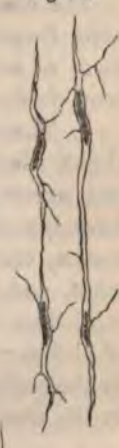


Fig. 26. Formative cells of the elastic fibres, × 350, from the tendo-achillis: *a*, of a four months' embryo; *b*, from a seven months' fœtus,—a few cells free, with one and two processes, others united by twos and threes.

Fig. 27. Stellate formative cells of the nucleus fibres out of the tendo-Achillis of a new-born infant, × 350.

the other hand, in those forms which still present indications of the original cells, a certain movement of the juices may still take place. Elastic tissue is not known to be regenerated, but new formations of it are not rare.

The elastic tissue is rarely found in large masses, but it is very frequently mixed with connective tissue, either in the form of isolated fibres or of networks of various kinds. As true *elastic organs* we may mention:

a. The *elastic ligaments*, in which the tissue, with only a slight admixture of connective tissue and hardly any vessels and nerves, exists, so to speak, in a pure form. As such we have the *ligamenta subflava* of the vertebræ, the *ligamentum nuchæ*, certain ligaments of the larynx, the stylo-hyoid ligament, and the *ligamentum suspensorium penis*.

b. The *elastic membranes*, which appear in the form either of fibrous networks or of fenestrated membranes, and are found in the walls of the vessels, especially in those of the arteries, in the *trachea* and *bronchiæ*, and in the *fascia superficialis*.

[In all the vertebrate classes the elastic tissue is found in the same localities as in man, and in a few particular situations besides, as in the ligaments of the cat's claw, in the alary membrane of mammals, in the folds of the alary membrane and in the lung sacs of birds. In the Invertebrata this tissue appears to be rare, and it is not even certain that the elastic ligaments which occur in them (as, for example, in bivalves), agree anatomically and chemically with the elastic tissues of the higher animals.

Of the different parts belonging to the elastic tissues, the so-called nucleus-fibres of Gerber are almost alone those whose development has been examined. With regard to these, Henle's view, that they arise by the coalescence of elongated nuclei, was almost universally received, until lately Virchow and Donders nearly contemporaneously brought forward another conception. Both these authors proceed from the investigation of the connective tissue, and show that what in it have been held to be elongated, isolated, or more or less coalesced nuclei, are nothing more than fusiform or stellate cells, with fine processes, which closely surround a generally elongated nucleus, and are partly united into fibres or networks. With

regard to the development of these cells, Virchow deduces from Schwann's observations, and Donders from his own investigations, the result that the well-known fusiform cells in the rudimentary areolar tissue of embryos are nothing more than the formative cells of the so-called nucleus-fibres; to which, then, as a consequence, it is added that the proper connective tissue does not proceed from cells, but is nothing else than fibrillated cytoblastema. Hence both these authors agree in placing connective tissue and cartilage side by side and, in comparing the formative cells of the so-called nucleus fibres, which Virchow calls "connective-tissue corpuscles," (Bindegewebskörperchen,) with the cartilage-cells; the interstitial substance of the cartilage, with the fibrous part of the connective tissue. Virchow goes still further, and compares even the bone substance to connective tissue; especially that which is developed by the ossification of what I have called soft blastema, in which the bone cavities, he supposes, proceed from stellate anastomosing "connective-tissue corpuscles," a view which seems chiefly to have led him to declare that the nucleus-fibres are hollow, and form a great system of tubules and cavities through the connective tissue, thus probably subserving nutrition. It could be imagined that the nutritious fluid might thus be quickly conducted for considerable distances, and uniformly distributed through the tissue, in which case the nuclei must be considered to be the special regulative portions of the apparatus, while the cells are simply conductors.

If we submit these different views to the test of observation, it results that much is quite correct, but that some points are untenable. It is true, that the so-called nucleus-fibres are developed from cells; and the fact is, indeed, noted in certain earlier statements and figures of Valentin, Hassall, Quekett, and others. In the tissues of full-grown animals, it is in many localities unquestionably impossible, in others very difficult, to attain to certainty upon these points, because here, even when the nucleus-fibres still present indications of cells, the cell-membrane so closely embraces the elongated and by no means vanished nucleus, that it is often quite out of the question to decide whether we have a cell with two or more slender processes, or a fusiform or stellate nucleus; on the other

hand in young animals, in which also Virchow made his first observations, and especially in embryos, it is easy to come to a clear decision upon the matter. In man, I find the tendons, ligaments, and the *aponeurosis palmaris* and *plantaris*, to be especially serviceable objects; but in all the places in which elastic tissue is mixed with connective tissue, I was able to follow their development. The observation is most successful in the fœtus of three to four months. Here, in all the more solid organs composed of connective tissue,—tendons, ligaments, fasciæ, corium,—the proper connective-tissue fibrils are already quite well developed, while of nuclear fibres, so to speak, there are no traces. Instead of these, however, we find between the often very distinct bundles of connective tissue, a great number of fusiform cells of 0·01‴—·015‴ in length, which in their middle (of 0·002‴—0·003‴ in breadth) inclose an elongated roundish clear nucleus with a nucleolus, which completely fills them, and are prolonged at their ends into fine dark threads. If we trace these cells, among which are always scattered many round and elongated cells out of which they are formed, and in older embryos a few stellate ones, with from 3 to 5 processes, it is found that they gradually become longer and narrower, and from the sixth month begin to coalesce with one another into elongated fibres or networks; up to a late period, however (even 7 to 8 months), these formative cells of the elastic tissue may be easily isolated in abundance from all forms of connective tissue, either singly or combined by twos and threes. In the fœtus at birth this can no longer be done; but here the complete nucleus fibres, at least in the more solid forms of connective tissue, still clearly exhibit their composition out of fusiform and stellate cells with nuclei; which, as we have already seen, is occasionally in some localities even the case in the adult.

What holds good of the nucleus fibres may be asserted also of the elastic fibres, which are not further treated of by Donders and Virchow. Valentin (Wagner's 'Handw. d. Phys.,' I, p. 668) found that the elastic fibres of the *ligamentum nuchæ* of the calf are considerably finer than those of the ox, and I stated ('Zeitschrift für Wiss. Zool.,' I, p. 77, Anm.) that all the thick elastic fibres of the adult have at one time been common nucleus-fibres. In fact, we find in the new-born

child not a single true elastic fibre, since even those of the *ligt. nuchæ*, of the *ligt. flava*, and of the aorta, when largest, do not measure more than 0·0008—·001‴. This circumstance alone, might, if we take into account the close resemblance of the elastic and so-called nucleus-fibres in other respects, be considered as a demonstration that the former are also developed out of cells, but we have in addition direct evidence that this is their mode of development.

In the aorta, in the *ligt. nuchæ*, and in the *fascia superficialis abdominis* of human embryos of the fourth and fifth months, we find the same short fusiform cells as in the common connective tissue; and their coalescence into originally finer fibres, though perhaps not quite so readily demonstrable as in the former localities, may yet be made out with certainty, so that the agreement in their genesis of the finer with the coarser elastic fibres, may be considered to be established.

Not, however, to the same extent, as with regard to the genesis of the finer elastic fibres, can I agree with the authors mentioned in other points. In the first place, concerning the physiological import of the so-called nucleus fibres, I grant to Virchow that even in the adult, in some places, they appear to retain more their original character of a system of canals; yet I can by no means allow, that these nucleus-fibres are to be regarded as a system of tubules subserving nutrition. In my opinion, all fine elastic fibres, which no longer present any trace of the original cell, *i. e.* those of the areolar connective tissue of the *corium*, *fasciæ*, of the *perimysium*, of the *periosteum*, of the *dura mater*, of the serous membranes, of the walls of the vessels, and of mucous membranes, are solid fibres, and only of service to the organism so far as they are elastic.

A relation to nutrition can only be supposed of those elastic elements of the tendons, ligaments, and of the cornea, which present conditions more nearly embryonic; but even with respect to these it does not appear so evident that it can be decidedly affirmed. In the tendons and ligaments, for instance, it is plain that a part only of the elastic elements are not quite fully developed, so that possibly cavities may still exist in them; while the rest, much more considerable, are as completely developed as elsewhere, and offer no trace of a cavity.

If, now, it were assumed that the former have a determinate relation to the conduction of the nutritive fluid, it would yet remain unexplained why, in certain regions, these organs were more favoured than in others. If it be further considered, that in the tendons and ligaments, as in the connective tissue in general, vegetative molecular changes and nutrition are assuredly at their lowest stage,—furthermore, that the arrangement of the nucleus-fibres (their more longitudinal course, the want of anastomosis of the nucleus-fibres of the different secondary bundles in tendons) appears very little fitted to conduct nutritious fluids from the surfaces of these organs, where only the vessels are found, into their interior,—there will appear no great necessity for entering further into this hypothesis. For the cornea alone, where the elastic tissue remains in a quite embryonic stage, should I be inclined to adopt Virchow's hypothesis; and, as respects the other tissues, I can only grant that, when the elastic elements are in such an imperfectly developed condition that they still contain canals for greater or less distances, they may have a share in the distribution of the nutritive fluid which naturally interpenetrates these organs, and, therefore, in their nutrition, but that this must rather be regarded as a secondary function, and will not justify their approximation to the fine canals of the teeth and bones, which exist specially for the purpose of nutrition.

Such a function might much rather be ascribed to the undeveloped nucleus-fibres and their formative cells in the immature (pathological or normal) connective tissue; for here, at least, the anatomical and physiological relations of the tissue are not opposed to such an assumption; it would amount to little more, however, than what may be asserted of every undeveloped fibrous tissue.

A second and much more important point in which I differ from Donders and Virchow is the general mode of looking at the connective tissue. Both these writers hold that it is not composed of cells, but is developed by the fibrillation of a homogeneous cytoblastema; and they believe that all the fusiform embryonic cells, which since Schwann's time have been regarded as its formative cells, belong not to it, but to the elastic tissue. I can by no means admit such a view, and it

seems to me to be comprehensible, only when we recollect that these authors arrived at it more upon theoretical grounds, than by direct observation. With Virchow, a passage in Schwann appears to have been conclusive, where he describes the embryonic connective tissue as a gelatinous homogeneous mass, which dissolves upon boiling, and contains cells distributed through it which are not affected by the boiling. Virchow does not hesitate to extend this to all connective tissue, and to assume that the substance soluble in water answers to the subsequently fibrous connective tissue, while the insoluble cells are the formative cells of the so-called nucleus-fibres. Here, however, he has omitted to notice, that Schwann speaks only of a determinate form of tissue, the *lax* or *areolated*, and describes in a totally different manner the formation of the more solid connective tissue, *e. g.* of a tendon. In this case we find, in direct contrast to the former, no trace of cytoblastema, which can in no way be directly observed, the tendon consisting throughout of fibre-cells, either isolated or united into bundles of connective tissue.

To observe this, however, the examination must be made at a very early period, since, as Schwann has justly remarked, the elements of the fibrous tissue are very early developed; a circumstance from neglecting to observe which, it seems that Donders has been led to adopt the same view as Virchow. For my own part I have found Schwann's statements confirmed in all essential points, with the single exception that he was unacquainted with the formative cells of the elastic fibres, and confounds them with those of the connective tissue. My observations upon these points are to be found in the following section. Hence I cannot admit that cartilage and connective tissue are nearly allied, inasmuch as the fundamental substances of both, even if chemically agreeing, yet, genetically, are very different.

Literature.—A. Eulenberg, 'de tela elastica,' 1836; Virchow, 'die Identität von Knochen, Knorpel und Bindegewebskörperchen, sowie ueber Schleimgewebe,' in the 'Verhandlungen der Phys. Med. Gesellschaft in Würzburg,' Bd. II, 1851, p. 150; and 'Weitere Beiträge z. Kenntniss d. Structur der Gewebe der Bindesubstanz.' Ebend. II, p. 314; Donders in the Nederlansch Lancet.,' 1851, July and August; and in the

'Zeitschrift für wissen. Zool.,' Bd. III, p. 348; Kölliker, 'Ueber die Entwicklung der sogenannten Kernfasern, der elastischen Fasern und des Bindegewebes;' in 'Verh. d. Phys. Med. Ges. in Würzburg,' Bd. III, H. 1.

§ 24.

Connective Tissue.—The elementary parts which are found in connective tissue may be divided into the essential, never-failing components, and those which are met with only in certain localities. To the former belongs the fasciculated as well as the more homogeneous connective tissue; to the latter, elastic fibres in their different forms and conditions of development, fat cells, cartilage cells, and pigment cells of different kinds. Besides these, connective tissue contains also no inconsiderable quantity of a gelatinous intermediate substance. The bundles of the connective tissue are, among the essential elements, those which occur most frequently; each of them consists of a certain number of very fine fibrils, the connective fibrils, which are distinguished from their nearest allies, the finest elastic fibres and muscular fibrils, by their smaller diameter (0·0003‴—0·0005‴), their pale colour, their homogeneous appearance, and the complete absence of striation. They are united by means of a small quantity of a clear connecting substance, and thus form the bundles in question, which in many respects resemble those of

Fig. 28.

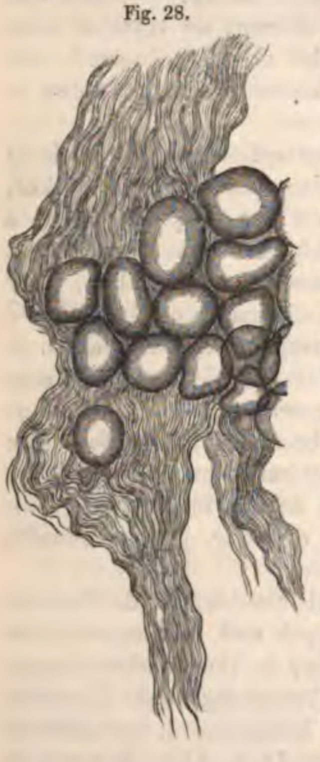


Fig. 28. Lax connective tissue with fat-cells from man, ×350.

the transversely striated muscles, but differ from them in the absence of any special investment comparable to the sarcolemma, and in their smaller mean diameter (0·004‴—0·005‴). They are either long, slightly wavy cords, of uniform thickness throughout, which are not directly connected together, but arranged in different ways near and above one another, forming great lamellæ and bundles; or they coalesce like the elastic networks into meshes, and thus form what I have called the *reticulated connective tissue*. In rare cases the bundles appear not to be composed of fibrils, but are more homogeneous, as in the neurilemma, where they are known as Remak's fibres. Besides this form of connective tissue, there exists a second, rarer kind, in which neither bundles nor fibrils can be clearly distinguished, but only a membranous or more or less solid, finely granulated, or slightly striated, even perfectly homogeneous, clear tissue; *homogeneous* (or Reichert's) *connective tissue*. The other elements which occur in connective tissue present nothing remarkable, and will be more particularly treated of in their proper places in the special part.

The chemical relations of connective tissue are well known: proper connective substance when boiled yields common gelatine, and contains besides a fluid, whose nature, on account of its generally minute quantity, cannot be investigated. Only where it exists in considerable proportion, as in the gelatinous connective tissue of embryos, can the presence of much albumen and mucus be easily demonstrated in it. The chemical qualities of the other constituents of the connective tissue will be spoken of in their place.

Connective tissue is of utility to the organism according to its composition,—sometimes as a solid unyielding substance; sometimes as a soft support for vessels, nerves, and glands; sometimes, finally, as a yielding tissue, filling up spaces and facilitating changes of position. Where elastic elements are present in it in great quantities, its nature alters; and a great abundance of fat or cartilage cells gives it an unusual softness or resistance. The connective tissue is invariably developed from cells, and, in fact, from fusiform or stellate vesicles, which become united into long fibres or networks, and often break up into fibrils before their union. The mode

Fig. 29.

Fig. 30.

in which this takes place is not yet quite made out, but it is most probable that the cells, as they elongate, change, with their membrane and contents, into a homogeneous softish mass, which subsequently breaks up into a bundle of fine fibrils and some intermediate substance. The development of the homogeneous connective tissue has as yet been little investigated, but it would seem, like the other, to proceed from a fusion of rounded or elongated cells, which are perhaps united by an intermediate substance, in which the metamorphic process has only gone so far as the development of a homogeneous mass, but has not attained the stage of fibrillation. The bundles of the connective tissue, when once formed, grow in length and thickness like the elastic fibres, until they have attained the size which they possess in the adult; however, there arise subsequently, in many places, additional elements, which are combined with the original ones. The perfect connective tissue, when unmixed, is almost non-vascular, and with regard to nutrition, is certainly very low in the scale, whence it undergoes hardly any morbid changes. The vascular connective tissue is an exception to this rule, but the changes in this case depend not upon any peculiarity in the connective tissue itself, but are determined by the vessels, fat-cells, &c. contained in it. The bundles of fibrils of the connective tissue and the

Fig. 29. Formative cells of the connective tissue from the skin of the trunk in a sheep's embryo, $7'''$ long, $\times$ 350: *a*, cell without any indication of fibrils; *b*, with commencing; *c*, with distinct fibrils.

Fig. 30. Three formative cells of the areolated connective tissue from the allantois of a sheep's embryo, $7'''$ long, $\times$ 350.

elastic fibres stand at the bottom of the series of the higher elementary parts, and thence most readily adapt themselves to the regeneration of lost substance, or to the increase of parts which already exist.

The union of the different elements of the connective tissue is effected in many ways, but the following forms are most worthy of distinction:

1. *Solid connective tissue* (formed connective tissue, Henle). In this the elements are intimately united, and in such a manner, that simple organs of well-marked form proceed from them. To this belong:

a. The tendons and ligaments, with parallel bundles, united by loose connective tissue, into larger cords, between which a relatively very small number only of fine elastic fibres, and fibrous networks, penetrate.

b. The fibro-cartilages have the same structure as the tendons and ligaments, but with numerous scattered cartilage cells, and without finer elastic fibres. They exist either as special organs, such as the *cartilagines interarticulares* and the cotyloid ligaments, or in particular parts of other organs composed of connective tissue, especially in the tendons, the tendinous sheaths, and the ligaments.

c. The fibrous membranes are distinguished from *a*, only by the frequent interweaving of the bundles, and generally by the more considerable number of the elastic fibres. Here may be enumerated:

1. *The muscular fasciæ*, which have more the structure of tendons.

2. *The periosteal membranes* and the *perichondrial membranes*, containing sometimes a great number of elastic elements.

3. *The white dense tunics of many soft organs*, as the *dura mater*, the neurilemma, the sclerotic and cornea, the fibrous coat of the spleen and kidneys, the *tunica albuginea* of the ovaries and *testes, penis* and *clitoris*. In the last-mentioned parts, and in the spleen, these coats, which consist of a solid connective tissue and numerous fine elastic fibres, are continued into the interior, where mixed to some extent with smooth muscles, they constitute a more or less complete frame-work, which appears in the form of partitions, or of a stroma, or of a

trabecular network. In the cornea we find a modification, inasmuch as the connective tissue is transparent, contains fine elastic tissue in a more embryonic state, and when boiled in water yields chondrin, and not gelatine.

d. The serous membranes consist of a connective tissue, rich in fine elastic fibres, whose bundles anastomose, or are interwoven in different modes; and sometimes also, especially at the surface of these membranes, appear more homogeneous. The serous membranes, which never possess glands, and upon the whole but few vessels and nerves, line the cavities which contain the viscera, and present an inner surface, which is smooth and shining from the presence of an epithelial investment. They do not necessarily form closed sacs, as was formerly believed, but may have apertures in certain localities (abdominal aperture of the Fallopian tubes), or may be wholly wanting, as upon the articular cartilages; or the areolar foundation may be absent, as in the so-called external lamina of the *arachnoidea cerebri.* To these membranes belong, 1, the *true serous membranes,* as the *arachnoidea,* the *pleura,* the *pericardium,* the *peritonæum,* and the *tunica vaginalis propria,* which all, normally, secrete only a minute quantity of serous fluid; and 2, the synovial membranes or capsules of the joints, *bursæ mucosæ,* and tendinous sheaths, which afford a viscid yellow secretion,—the *synovia*—containing albumen and mucus.

e. The corium consists of a dense network of bundles of connective tissue, which at the surface, and in the papillæ, gives place to an indistinctly fibrillated, in part even more homogeneous tissue, and contains a great quantity of finer and coarser elastic networks, as well as very numerous vessels and nerves.

The *corium* supports the papillæ upon its outer surface, and is here covered by the epidermis, in connection with which it forms the external skin; from the deeper parts it is separated by a soft tissue, generally very rich in fat, the subcutaneous connective tissue, adipose membrane, or *panniculus adiposus.*

f. The mucous membranes essentially consist of a very vascular basis of connective tissue, well supplied with nerves,—the proper mucous membrane—of an epithelial layer covering it, and of a submucous areolar tissue, which

in the intestine is also called the *tunica nervea*. The former is of the same structure as the *corium*, only softer, and not unfrequently poor in elastic tissue. The mucous membranes are distinguished from the serous, in general by their greater vascularity, their more considerable thickness, their numerous glands, and the mucous secretion, which may be especially ascribed to their soft epithelium; though there are mucous membranes which are as delicate and glandless as serous membranes; and, on the other hand, the synovial capsules may approximate the mucous membranes in their vascularity and the nature of their secretion. The mucous membranes and the external skin are analogous in all their principal components, whence the transitions between the two, such as exist upon the lips, eyelids, and elsewhere, are not surprising. To the mucous membranes belong the innermost coat of the *tractus intestinalis;* the lining of the nasal passages, and of their secondary cavities; the Eustachian tube, the *tympanum* and mastoid cells, and the conjunctiva. Among the glands, all the larger, present in their excretory ducts, a distinct mucous membrane, as the lungs from the *glottis* to the finest *bronchiæ;* the liver in the larger gall-ducts and in the gall-bladder; the pancreas in the *ductus pancreaticus;* the urinary and sexual organs; in the urethra, bladder, ureters, pelvis of the kidneys, vagina, uterus, and oviducts; and in the ducts and follicles of the mammary gland; in the seminal vesicles and in the *vas deferens*. In all these glands the coats of the mucous membrane pass immediately into the walls of the glandular tubes and vesicles, which might thus be regarded as composed of a more delicate mucous membrane. The same might be said of the smaller glands, as those of the intestine, which are directly connected with the larger mucous expansions, only in that case the smaller glands of the skin must be regarded as attenuated processes of it. Inasmuch as both physiology and development support this view, it would seem to be at any rate justifiable; yet every one is free, notwithstanding, to look more to the differences which certainly do exist between the parts in question, and to consider them as distinct structures.

g. The membranes of the veins, lymphatics, the adven-

titious coat of the arteries, and the endocardium, consist of a loose connective tissue not altogether dissimilar to that of the fibrous membranes, and of finer or coarser elastic fibrous networks, with which in the veins smooth muscles are also partly mixed.

h. The so-called vascular membranes (*tunicæ vasculosæ*), to which belong the *pia mater,* with the *plexus choroidei,* the choroid coat and the iris, all contain very numerous vessels, which, however, appear to have less reference to the membranes themselves than to the nutrition of other organs. Supporting these vessels we have either a common connective tissue, in which there are no elastic fibres (*iris, pia mater*), with parallel, matted, and anastomosing bundles, or a homogeneous connective tissue (*plexus choroidei, choroidea*), to which, as in the choroid, peculiar elements, namely, anastomosing cells, generally filled with more or less pigment, may be added.

i. The homogeneous connective tissue.—In many organs we find membranes whose chemical nature agrees with that of connective tissue, but which contain neither distinct bundles nor fibres, and appear to be more homogeneous. Such is the homogeneous tissue which often invests the bundles of the arachnoid singly, or in a number together; the coats of the Malpighian corpuscles of the spleen, and of the glandular follicles of the intestine (tonsils, lingual-follicles, the solitary and Peyerian glands), certain of the so-called *membranæ propriæ* of the glands appear to come under this head also; yet, since some of them do not belong here, and consist of a very different substance from connective tissue, as, for example, that of the kidneys, and since we have no thorough investigation of these structures, for the present nothing decided can be said upon the subject.

k. Loose or areolated connective tissue ("amorphous connective tissue" of Henle), consists of a soft meshwork of reticulated, or variously interwoven bundles of connective tissue, which in larger or smaller quantity constitute a filling up and uniting mass between the organs and their parts, and appear under two forms:

1. As *adipose tissue,* when numerous fat-cells are contained in the meshes of an areolated tissue which is usually very poor in elastic fibres.

2. As *common lax connective tissue,* when the latter are

few or wanting. The adipose tissue occurs principally in the skin, forming the *panniculus adiposus;* in the larger cylindrical bones, as yellow bone-medulla; in the orbit; around the kidneys; in the mesentery and the omentum; around the spinal marrow; in nerves and vessels, and in muscles. The areolated connective tissue is widely distributed between the separate organs and viscera of the neck, thorax, abdomen, and pelvis, and everywhere along the course of the vessels and nerves, and in the interior of the muscles, nerves, and glands.

[The connective tissue is found in all the four classes of the vertebrata, in about the same condition as in man; while, on the other hand, in the invertebrata it is very rare, and when present is more homogeneous, or consists of isolated cells and intermediate substance, rarely more fibrous, as in Cephalopoda, in the mantle of bivalves, in the peduncle of the Lingulæ, and of the Cirripeds. Fat-cells also do not occur among the lower animals to the same extent as among the higher. The firm connective tissue is here replaced by a chitinous substance, or by one consisting of cellulose, and by calcareous or horny tissues.

Opinions are still divided as to the structure and development of the connective tissue. Whilst the majority ascribe a distinctly fibrous structure to it, and suppose it to consist of bundles, and these again of fibrils, Reichert considers this tissue to be more homogeneous, and regards the fibrillation partly as artificial, partly as the expression of a folding, a view to which Bidder and Virchow are also inclined. For my own part, I find a certain amount of truth in Reichert's conception, insomuch as it is not to be denied that there also exists a non-fibrillated, more homogeneous connective tissue, which had previously been little investigated; but I am nevertheless of opinion, that, as applied to the great mass of the organs composed of connective tissue, it is incorrect. The possibility of making out fibrils in delicate membranes, even without preparation, the ease with which these may be isolated in tendons and ligaments, and lastly, the circumstance that the fibrils may be demonstrated upon transverse sections of the tendons, and of the more solid connective tissue in general, are for me sufficient reasons for retaining the old view.

With respect to the *development* of the connective tissue, I

distinguish two types which correspond with its two principal forms, the solid and the areolated. The former is developed out of masses of cells without any demonstrable matrix, by the elongation of the cells, their breaking up into fibrils, and their coalescence. This is most obvious in the tendons and ligaments, which, as observations upon Batrachian larvæ and upon mammalian embryos show, at first consist entirely of common, rounded, formative cells, which about the same time as the transversely striated muscles are formed, (in mammalia in the second month) become fusiform. The further development demonstrates (what had escaped Schwann) that only one portion of these fusiform cells, and in fact cells which are remarkable for their size and paler contours, become bundles of connective tissue, while the others, which Schwann in part depicts rightly (Tab. III, fig. 11; the smallest cell, fig. 6, from connective tissue, the cell *b*, and the lowest cell upon the right side), remain for a time as fusiform elements, and only subsequently become fused into elastic fibres. There arises, at last, out of cells alone, with no distinguishable matrix, a compact tissue composed of two chemically quite distinct fibres. The *areolated connective tissue* differs from the former in the circumstance that, if not from the beginning yet from the time at which the cells become elongated, an abundant gelatinous intermediate substance is developed between them, which does not yield gelatine, and never becomes converted into it, but contains albumen and a substance similar to mucus; Schwann, indeed, found a substance resembling *pyin*, in this tissue. Although all embryologists know that the areolated connective tissue is at first of a gelatinous consistence, as, for example, under the skin, in the neck, in the omentum, behind the peritoneum, in the orbit, and in the bones, no one has yet drawn attention to the general occurrence of that intermediate substance which was observed by Schwann in a single locality. I originally became acquainted with this tissue between the chorion and amnion, and at first paid more attention to its reticulated anastomosing cells. Subsequently, when I examined it more closely in the enamel organ of the embryonic tooth sac, I paid attention to the peculiar intermediate substance, and at the same time Virchow described this tissue from the umbilical cord, where the gelatinous tissue of Wharton

entirely consists of it. Virchow believed that it ought to be distinguished from connective tissue, and proposed the denomination of mucous tissue (*tissu muqueux*) for it. I considered it from the first to be connective tissue, and I now feel the more inclined to remain of this opinion, because I find that every description of the areolated connective tissue of embryos originally commences under this form, and therefore the circumstance that the tissue in the umbilical cord never arrives at perfection, cannot determine its nature.

The mode in which the *gelatiniform connective tissue* is developed is this: one portion of the cells contained in the gelatinous basis changes into connective tissue by becoming fusiform, and breaking up into common or reticulated, anastomosing connective tissue, which however, as Schwann has already stated, at first yields no gelatine. In this manner a closer or denser network arises, in the interspaces of which the intermediate substance or matrix, and a remainder of the previous formative cells, are contained. In the further course of development, new cells proceed from the matrix, which hereby diminishes by degrees in quantity, and at the same time the original network consolidates, fresh cells being added to it, a part of which also become elastic fibres and vessels. If subsequently the areolated connective tissue includes no adipose cells, the gelatinous tissue ends by completely disappearing, and nothing remains but a loose fibrous tissue, containing at most somewhat less fluid, and loose cells in its meshes; if, on the other hand, it becomes converted into an adipose tissue, the spaces remain, and a great part of the cells which have arisen at the expense of the gelatinous substance, subsequently pass, by the development of fat in their interior, into fat-cells.

In the gelatinous tissue of Wharton, between the chorion and amnion, and in part in the enamel organ, the areolated connective tissue remains more in its fœtal condition of a gelatinous tissue, yet there exists no natural line of demarcation from ordinary connective tissue, so much the less, since in the gelatinous substance of Wharton, in older embryos even fibrils are quite evident, and in the enamel organ the passage of a part of the gelatinous tissue into common connective tissue is demonstrable.

So much for the two types of development of the connective

tissue. We have yet to state how the bundles become chemically and morphologically what they are. In the first place, I may observe that the formative cells of the connective tissue are not originally distinguishable from the other formative cells of the embryo, do not dissolve by boiling in water, and therefore contain no gelatine. Even when the cells have evidently become fusiform, and have already coalesced into bundles and networks, they still, as Schwann has already stated, yield no gelatine. Therefore, in this case, the change of the cells into a collagenous substance, goes on as slowly as in the matrix of the cartilages, which, according to Schwann, also, at first, yields no gelatine, and therefore it is no objection to the above view of the nature of Wharton's gelatinous tissue, that it yields no gelatine on boiling, as Scherer has found. How the collagenous matter is formed out of cells, whether the contents only, or the membrane also, takes part therein, it is very difficult to say; in any case, from what we know of the contents of embryonic cells, it can hardly be any but a protein substance which yields the gelatine, and, from what takes place in the ossification of the cartilage cells, it seems very probable that the cell-membranes and contents together become metamorphosed into a collagenous substance.

The morphological change, which the formative cells of the connective tissue undergo, in the course of their passage into bundles of fibrils, is very probably this, that after their membranes and contents are fused into a homogeneous semi-solid mass, they then secondarily break up into fibrils; the latter process taking place in the same manner as we see it occur in the contents of the animal muscular fibres. Herewith, as a rule, the nuclei of the cells eventually disappear, or if they remain, as we see occasionally in connective tissue, still they never become changed into the so-called nucleus fibres.

Though in physiological connective tissue, development from cells must be most decidedly affirmed, it does not therefore follow that a substance which chemically and morphologically closely resembles connective tissue, may not arise in a different manner. We know, in fact, that the collagenous basis of cartilage, when it breaks up into fibres, becomes deceptively similar to connective tissue, and furthermore, that fibrous exudations may become changed into a fibrous substance which

is scarcely, perhaps not at all, to be distinguished from genuine connective tissue. There also exists, however, *a pathological true connective tissue in cicatrices of all kinds, and perhaps elsewhere, which is developed from cells;* and for my own part, therefore, I am opposed to the classing together of all connective tissues. We must in our classifications not only distinguish similarity or identity in structure and chemical composition, but embrace all the conditions, and especially the genesis; and thence we must distinguish both the collagenous fibrous cartilage and the collagenous organised fibrine, from true connective tissue,—just as we separate the true elastic fibre, from the chemically and morphologically, very similar fibres of the reticulated cartilages and from certain forms of metamorphosed fibrine. On the other hand, the connective tissue which has not been developed from cells may justly and properly be arranged with cartilage.[1]

[1] [The arguments brought forward by Professor Kölliker in support of his views with regard to the nature and mode of development of connective tissue, appear to us not to preponderate against those of Reichert, Virchow, and Remak, and to be opposed to our own observations, which agree in all essential points with those of the last-named authors.

There are two questions in dispute. The first, the structure of the connective tissue; the second, the homology of its various constituents with those of other tissues, and of cells in general.

With respect to the first question, it is admitted on all hands that ordinary connective tissue (*e. g.* of the tendons) is composed of two elements: *a*, a network of elastic tissue, which is not acted upon by cold acetic acid; *b*, a substance which is swollen up by acetic acid, and has a more or less fibrillated *appearance*, contained in the meshes of the elastic tissue. Now it has been demonstrated by Virchow, and the fact is admitted by both Kölliker (*supra*) and Reichert (Zur Streitfrage über die Gebilde der Binde-substanz, über die Spiralfaser, &c., Müller's 'Archiv,' 1852), that the elastic fibres are originally cells, and therefore that they are homologous with the cartilage-cell, *i. e.* the cartilage-cavity with its wall *plus* the cartilage-corpuscle or nucleus. That this is the case is very evident, upon examining in a young animal (*e. g.* kitten) the insertion of the tendo-Achillis into the cartilaginous extremity of the *os calcis*. It is here easy enough to see that the oval or rounded cells of the true cartilage pass in the most gradual manner into the elongated elastic fibres of the true tendon. The cells retain their cavities for a considerable time, but eventually the nuclei and the thin layer of substance which immediately forms the wall of the cavity, become fused into one mass and altered in chemical composition. A like alteration affects the matrix in various irregular directions, so that the delicate elastic connecting fibres are formed, and constitute a network through the whole tendon. These connecting fibres are often branched, and even appear fibrillated at the ends, especially if torn out from their connection with one another, and in this condition they exactly resemble the bodies figured by Professor Kölliker as the "fusiform formative cells" (fig. 29). That they have nothing to do

Literature.—C. B. Reichert, 'Vergleichende Beobachtungen über das Bindegewebe und die verwandten Gebilde,' Dorpat, 1845; Luschka, 'Die Structur der serösen Häute.' Besides which, consult the works of Virchow, Donders, Remak, and myself, cited above.

with the development of the "fibrillated" collagenous substance is, however, obvious, from this very simple circumstance—that the latter lies between them, and in part replaces the rest of the matrix of the cartilage, into which it can be directly traced. It will not be said in this case, that the "fibrillated" tissue of the tendo-Achillis is only "deceptively similar" to true connective tissue—and yet the transition of true cartilage into true connective tissue, is not less certainly demonstrable in the intervertebral cartilages, &c.

As Reichert, then, long since indicated, in illustrating his "*law of continuity*," (a law whose full importance, it may be observed, has yet to be developed), and as he and Virchow have since demonstrated, the elastic element of fully-formed connective tissue represents the cartilage-cells, while the collagenous element represents the matrix of the cartilage, and is not developed from distinct cells.

With regard to the structure of the latter element, Reichert, in his last communication, after considering Kölliker's arguments, denies the truth of his statement, that the ends of the fibrils may be seen in transverse sections of the tendons (§ Tendon, *infra*), and retains his opinion that it is not truly fibrillated in the uninjured state, but that it is simply plaited. Some remarkable observations upon the behaviour of the "connective fibril bundles" with acids and alkalies, to which Reichert first drew attention in 1846, and which have been since extended by Dr. Paulsen (Bericht., Müller's 'Archiv,' 1849), are, as the former points out, of the greatest importance in determining the nature of this tissue, and remind one somewhat of the equally puzzling structure of the starch-corpuscle. Dr. Paulsen states, that if a piece of tendon be kept for twenty-four hours in a solution of caustic potass of 10 per cent. strength, it changes into a viscid hyaline mass, so transparent that it can hardly be distinguished from the surrounding fluid. This substance can be torn with equal ease in any direction, and no fibrous structure can in any way be detected in it. Under the microscope the mass is quite transparent, and shows no trace of the well-known striation. However, the connective tissue is at this time by no means dissolved, nor is its texture destroyed. If the potass be removed by acetic acid, and this if it be in excess, by washing, the original texture returns. The author justly remarks, that if the connective tissue consisted of separate fibrils the impossibility of isolating them in the distended condition would be quite inexplicable. It is however intelligible, that in consequence of such an alteration in the connective tissue its cleavability may be diminished or destroyed, which does away with the necessity of supposing a fibrous structure. On the other hand, if a piece of tendon be hardened by a strong solution of caustic potass, or by nitric or hydrochloric acids, no fibres can be demonstrated in it (Bericht, pp. 40, 41). It is easy enough to verify the truth of these statements, by treating a piece of tendinous tissue with acetic acid, when, as is well known, the fibrillated appearance disappears; then keeping in view one of the distended and transparent "bundles," slowly add a solution of caustic ammonia, the transparent mass will be seen gradually to shrink, and eventually to resume, what appears to be, a most distinctly fibrous appearance.

The *gelatinous or rather gelatiniform areolated connective tissue* of Professor

§ 25.

Osseous Tissue.—Morphologically, the osseous tissue consists essentially of a matrix, and, scattered through it, of a multitude of microscopic cavities, the *bone corpuscles*, or *lacunæ*, of 0·006—0·014''' in length, 0·003—0·006''' breadth, and 0·002—0·004''' thickness. The former, of a white colour, is

Fig. 31.

Fig. 31. A portion of a perpendicular section of a parietal bone, × 350: *a*, lacunæ with pale only partially visible canaliculi, filled as in the natural condition with fluid; *b*, granulated matrix. The striated parts indicate the boundaries of the lamellæ.

Kölliker is simply ordinary connective tissue, in which the collagenous element is not yet or but little formed. Its development may be readily traced in the most superficial layer of the skin and mucous membranes, or in the tooth-pulp, or the so-called *actinenchyma* of the enamel organ in the calf, &c. The epiglottis of the kitten is particularly to be recommended, as this tissue can be observed passing on the one side into the homogeneous layer of the corium next to the epithelium, and on the other into the so-called fibro-cartilage of the epiglottis.

In all these cases, the mode of development of the areolated connective tissue is essentially similar to that observed by Remak (Ueber die Entstehung des Bindegewebes, &c., Müll. 'Archiv,' 1852, I,) in the Frog. The layer of the tissue next the epidermis or epithelium, is composed of a nearly homogeneous substance (matrix), in which lie corpuscles (so-called *nuclei*), the whole in fact corresponding exactly with embryonic cartilage. Internal to this, vacuolar cavities have been formed in the matrix between the corpuscles, the substance of the matrix appearing as bands or fibres between these *vacuolæ*. The latter enlarging, the substance of the matrix is more and more broken up into bands, in which dilatations remain where the "nuclei" are situated, so that the bands often resemble fusiform or stellate cells. A structure of this kind which undergoes no further chemical or morphological alteration, constitutes the *gelatiniform connective tissue;* and it is unquestionable, that its subsequent conversion into perfect areolated connective tissue is effected, as Professor Kölliker states, by the direct passage of these fusiform bodies into the pseudo-fibrillated bundles of the collagenous substance. But it is their outer portion only, that therefore which corresponds with the matrix of cartilage, which becomes thus changed—the elastic element being developed as before, not from separate cells, but by the chemical metamorphosis of the matrix immediately around the cavity which contains the "nucleus," and in various other directions.

That the pseudo-fibrillated portion of the connective tissue corresponds with the matrix of the cartilages is then, we think, certain. Whether with Remak we are to regard both these as cell-walls, or with Reichert as intercellular substances, must be discussed hereafter. (*See* General Appendix.)—Eds.]

sometimes more homogeneous, sometimes finely granular, very frequently lamellated, and hard and brittle from its being intimately combined with calcareous salts; the *lacunæ* are for the most part lenticular, and are united by very numerous fine processes, the *canaliculi*; by which some of them also open upon the outer surface of the bones and into the larger and smaller medullary and vascular spaces in the interior. The *lacunæ* and *canaliculi* contain a clear substance which may be regarded as the nutritive fluid of the bones, and besides, a cell-nucleus appears in many cases, perhaps constantly, to be inclosed within the lacunæ. Besides these two most essential elements, which exist in all bones, numerous vessels and nerves occur in most, as well as, frequently, a peculiar substance, the *medulla*, which supports them, and consists either of common fatty tissue, or of a loose, scanty, connective tissue, with few fat cells and many peculiar, so-called medulla-cells. These soft parts fill up the larger cavities in the interior of the bones and in the spongy substance; but are to be found also, at least partially, in narrow canals which penetrate the compact substance, *the vascular* or *Haversian canals*, which open in all directions upon the outer and inner surfaces of the bones.

The *matrix* of the osseous tissue is composed of an intimate combination of an organic substance, which perfectly agrees with that of the connective tissue, and of inorganic compounds, among which the phosphate and carbonate of lime are the principal constituents. The fluid contained in the cavities and canals is not thoroughly understood, but it probably presents a preponderance of albumen, fat, and salts, like the serum. The bones, from their solidity and inflexibility, serve as supports to the softer organs or for their more secure inclosure; and also perform special functions; as, for example, the auditory ossicles and the parts of the labyrinth which conduct the sonorous vibrations. The development of the bones takes place in two modes; firstly, by the metamorphosis of genuine cartilage, and secondly, by that of a soft blastema composed of indifferent cells and of a fibrous

Fig. 32.

Fig. 32. Six developing bone-cells from a rickety bone, as yet sharply defined from the interstitial substance: *a*, simple bone-cells; *b*, compound ones running to a parent cell, with two secondary cells; *c*, such arising from three cells, × 300.

substance similar to connective tissue. In both cases it is the cells—in the one the cartilage cells, in the other, cells without any defined character—which form the *lacunæ* and *canaliculi* by the thickening of their walls, with a contemporaneous development of pore canals, which subsequently grow into the matrix and unite with one another; whilst the matrix of the cartilage and the fibrous substance harden into the matrix of the bone by the deposition of calcareous salts, which likewise infiltrate the thickened cell-walls. The nutrition of the bones is very energetic, and is effected by the vessels of the investing periosteum, and, if they be present, by those of the medulla and the Haversian canals also. The bones have a great capacity of regeneration, and readily unite; in fact, very great losses of substance are repaired, or even whole bones, if the periosteum be left: adventitious development of bone is also very common.

The osseous tissue is found, firstly, in the bones of the skeleton, to which also the auditory ossicles and the hyoid bone belong; secondly, in the bones of the muscular system, as the sesamoid bones and the ossifications of tendons; thirdly, in the *substantia osteoidea*, or tooth cement. Many cartilages ossify with tolerable regularity as they grow older; as the costal-cartilages, and those of the larynx.

Dentine may be regarded as a modification of osseous substance, which, instead of solitary *lacunæ*, presents long canals, —the dental canals; besides which, it exhibits some chemical modifications. The development of the dentine leads to the conclusion that it is an osseous structure, whose cells, in the course of their ossification and thickening, become united into tubes, and have very little or no intermediate substance; a view which gains additional support from the numerous transitional forms, to be observed in animals, between typical dentine and osseous tissue.

[In the Vertebrata, bone is found more extensively distributed than in man. It exists in the skin (Armadillo, Tortoises, Lizards, Fishes), in the heart (the cardiac bone of the Ruminants and Pachydermata), in the muscular system (diaphragmatic bone of the Camel, Lama, and Porcupine, ossified tendons of birds), in the eye (sclerotic ring of Birds, Chelonians and Saurians, bony scales of the sclerotic of many Fishes), in the external portion of

the nose (proboscis of the Pig and Mole, *os prænasale* of the Sloth), in the tongue (*os entoglossum* of Fishes and Birds), in the respiratory organs (laryngeal, tracheal, and bronchial bones of many Birds), in the sexual organs (*penis-bone* of Mammalia), in the osseous system (*ossa sterno-costalia* of birds and some mammals). In the Invertebrata true bones are never found, being, in them, replaced by the so-called *calcareous* skeletons, which principally consist of carbonate of lime, and arise in different structures as incrustations of homogeneous tissues and of cellular parenchymata, as solidifying excretions of calcareous matter, or as deposits of calcareous concretions. The teeth are limited to the three well-known classes of vertebrata. In the Plagiostomata, structures precisely similar to the teeth occur as cutaneous spines.]

Literature.—Deutsch, 'De penitiori ossium structurâ Observationes,' Diss. Vrat., 1834; Miescher, 'De inflammatione ossium eorumque anatome generali.' Accedunt observat. auct. J. Müller, Berol., 1836; Schwann, article 'Knochengewebe,' in 'Berl. encyclop. Wörterbuch der med. Wiss.,' Bd. xx, p. 102; Tomes, article Osseous Tissue, in 'Cyclop. of Anatomy,' vol. iii.[1]

§ 26.

Structure of the Smooth Muscles.—The smooth muscles consist essentially of microscopic, usually fusiform, more rarely shorter and broader fibres, to which I have given the name of "contractile or muscular fibre-cells." Each of these elements, in the mean from 0·02—0·04‴ long, 0·002—0·003‴ broad, is an elongated cell, wherein, however, no difference between contents and membrane can be distinguished; but which consists of an apparently homogeneous, often finely granulated or slightly striated, soft substance, in which without exception in the middle of the fibre a generally columnar elongated nucleus

[1] [While perfectly agreeing with Professor Kölliker's general view of the relations between *dentine* and *bone*, namely, that the canals in the former represent the cavities and canaliculi which exist in the latter structure, we do not think that his statement of the mode in which the process of calcification of the dentine takes place is correct. So far as we have seen, the dentine is never developed by the immediate ossification of cells, nor do the latter take any *direct* share in its formation. (*See* Quarterly Journal of Micros. Sc., April, 1852.) It may be said that dentine is bone, in which, in consequence of the early disappearance of the "nuclei" from the ossifying blastema, the *lacunæ* are not formed, the dentinal tubes presenting only the *canaliculi*.—Eds.]

exists. These fibre cells are united by means of a substance which cannot be directly demonstrated, into flattened or rounded cords, the bundles of the smooth muscles; which are then united, by delicate investments of connective tissue with fine elastic fibres (a kind of *perimysium*), into more considerable masses, in which numerous vessels and a relatively small number of nerves are distributed. Chemically, the principal constituent of smooth muscle is a nitrogenous substance similar to fibrin, the so-called *muscular fibrin* or *syntonin* (Lehmann), which, from the observations that have hitherto been made, is distinguished from blood fibrin only in this, that it is not dissolved by solution of nitre, nor by carbonate of potass, but very easily by dilute hydrochloric acid.

Fig. 33. Fig. 34.

The *physiological importance* of the smooth muscles lies in their contractile power; in consequence of which they afford considerable assistance to the functions of the different viscera. The development of their elements takes place simply by the elongation of rounded cells, the membranes and contents uniting into a homogeneous soft substance. The nutrition of the smooth muscles would seem to go on very actively, according to the later investigations upon the fluid which bathes them, which, according to Lehmann, has most generally a distinctly acid reaction, and together with lactic, acetic, and butyric acid, contains *creatin* and *inosit*; and the same conclusion may be deduced from the frequent occurrence of physiological (in the uterus) and pathological hypertrophies and atrophies of them. Whether smooth muscles are regenerated, or whether loss of their substance is replaced by a similar tissue, is unknown; on the other hand, new formations of them appear to occur in uterine tumours.

The smooth muscular fibres never form large

Fig. 33. Muscular fibre-cell from the small intestine of man.

Fig. 34. Muscular fibre-cell from the fibrous investment of the spleen of the dog, × 350.

isolated muscles in the human body; as, for example, is the case in the genito-rectal muscles of mammalia, but exist either scattered in the connective tissue, or in the form of *muscular membranes.* In both cases the bundles are either parallel or interwoven into networks. Their distribution is as follows:

1. In the *Intestinal canal* the smooth muscle forms: first, the *tunica musculosa* from the lower half of the œsophagus, where smooth bundles are still mingled with transversely striated fibres, as far as the *sphincter ani internus*: secondly, the muscular layers of the mucous membrane, from the œsophagus to the anus: and thirdly, scattered muscular bundles in the *villi.*

2. In the *Respiratory organs,* a layer of smooth muscles appears in the posterior wall of the trachea, and accompanies the *bronchiæ,* even to their finest ramifications, as a complete, circularly fibrous membrane.

3. In the *Salivary glands,* this tissue is found solely in Wharton's duct; and here only scantily, and forming an incomplete coat.

4. The *Liver* has a perfect muscular layer in the gall-bladder, and scattered smooth muscles, also in the *ductus choledochus.*

5. The *Spleen* has this kind of muscle in many animals in its outer coat, and in the *trabeculæ,* mixed with connective tissue and elastic fibres.

6. In the *Urinary organs* the smooth muscles are found in the *calices* and *pelves* of the kidneys, form a complete muscular layer in the ureters and urinary bladder, but are only sparingly to be found in the urethra.[1]

7. The *Female sexual organs* possess smooth muscles in the oviducts, the uterus, where during pregnancy their elements become excessively developed, and attain a length of $\frac{1}{4}'''$, the vagina, the *corpora cavernosa,* and in the broad ligaments of the uterus in different places.

8. In the *Male sexual organs* they are found in the *dartos,* between the *t. vaginalis communis* and *propria,* in the *vas*

[1] [Mr. Hancock (On the Anatomy and Physiology of the Male Urethra, London, 1852), who had made out the existence of the organic muscular layer in the urethra independently, attributes to it much more anatomical and physiological importance. (See below, § Urinary Organs.)—Eds.]

deferens, vesiculæ seminales, the prostate, around Cowper's glands, and in the *corpora cavernosa penis*.

9. In the *Vascular system* smooth muscles exist in the *tunica media* of all, especially of the smaller arteries; also in that of most veins, and of the lymphatics, with the exception of the finest; furthermore in the lymphatic glands (Heyfelder); and lastly in the *tunica adventitia* of many veins. The elements, in vessels of middle dimensions, are everywhere fusiform fibre-cells; in the large arteries, on the other hand, shorter plates, which often resemble certain forms of pavement epithelium; and in the smallest arteries they are more elongated, or even round cells, forms which must be considered as less developed.

10. In the *Eye*, smooth muscles form the *sphincter* and *dilator papillæ* and the *tensor choroideæ*.

11. In the *Skin*, lastly, this tissue appears besides in the *dartos*, in the form of minute muscles upon the hair sacs, in the areola, and in the nipple, and in many of the sudoriparous and sebaceous follicles.

[The elements of the smooth muscles were formerly universally regarded as elongated bands containing many nuclei, which were supposed to be developed by the coalescence of numerous mutually applied cells. In 1847 I showed that this is not the case; that, on the other hand, the elements of these muscles are only modified simple cells; and at the same time I demonstrated, that these contractile fibre-cells occur wherever contractile connective tissue had previously been assumed to exist, and also, that they are to be found in many localities in which their presence had not been suspected. These views, notwithstanding contradiction at first from certain quarters, are now universally confirmed; a result to which Reichert, by the discovery of a reagent, which readily enables even those who are less practised, easily to isolate the contractile fibre-cells, viz.: nitric and hydrochloric acids of 20 per cent. (Müller, 'Archiv,' 1849, and Paulsen, 'Obs. Microchem.,' 1849); and Lehmann, by his chemical investigations upon this tissue, have contributed their share. Contractile fibre-cells occur in all four classes of the Vertebrata, but appear to be wholly wanting in the Invertebrata, since the smooth fibres of these creatures, which have been

thought to be such, are allied genetically to the transversely striated muscles of the higher animals.

Their occurrence in the Vertebrata is in some respects peculiar, and I will here mention the following localities in which they are found: In the skin of Birds, as the muscles of the quill-feathers—in this case with tendons of elastic tissue; in that of the Orang-outan, in the hair-sacs, as in man; in the iris of the Amphibia; in the *campanula Halleri* of the osseous Fishes (Leydig); in the swimming bladder of Fishes; in the lungs of the Frog (in Triton they are here wanting); in the mesentery of the Plagiostomata, of *Psammosaurus* and *Leposternon* (Leydig u. Brücke); in the genito-rectal muscle of Mammals. In the gizzard of birds these muscles are of a bright red colour, and are united with a tendinous membrane.]

Literature.—Kölliker, 'Ueber den Bau und die Verbreitung der glatten Muskeln.,' in the 'Mittheilungen der Naturf. Gesellschaft in Zürich,' 1847, p. 18, and 'Zeitschrift für wiss. Zool.,' Bd. I, 1849; C. R. Walther, 'Nonnulla de musculis lævibus.,' Diss. Lips. 1851.[1] [Jos. Lister, 'Observations on the Contractile Tissue of the Iris,' Quart. Journ. Mic. Sc., vol. I, p. 8, Pl. i.—Eds.]

§ 27.

Transversely Striated Muscular Tissue.—The elements of this tissue consist essentially of the so-called muscular fibres or primitive muscular bundles, each of which, 0·004—0·03‴ thick, consists of fine fibrils surrounded by a special homogeneous, delicate, elastic investment, the *sarcolemma*: the fibrils

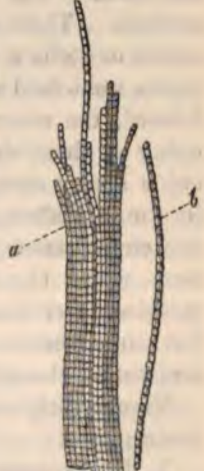
[1] [Reichert (Bericht, 1849, Müller, 'Archiv.,') states that, according to Paulsen, the action of a solution of caustic potass of 50 per cent. causes the smooth muscles to become wavy, and thus to assume a transversely striated appearance under the microscope. Macerated in such a solution for three days, they break up into small globules: striated muscle behaves in a similar manner, and the globules correspond in size to the interval between two striæ.

Eylandt (Obs. Microscop. de musculis organicis in hominis cute obviis. Diss. inaug., Dorp. 1850, c. Tab. lithog.), denies the existence of *free* smooth muscles in the *papilla and areola mammæ*, in the *scrotum*, in the skin of the penis or of the prepuce, and in the perinæum. Nor does he find them in the outer layers of the hair-sacs (apart from the *arrectores pili*), in the *glandulæ sudoriferæ* of the *axilla*, of the anus, &c., nor in the *glandulæ ceruminosæ*. The smooth muscles observed in the *papilla and areola mammæ*, in the skin of the penis and of the perinæum, he considers to belong to a greatly developed vascular layer. (See, however, the remarks of Prof. Kölliker upon Eylandt's statements, at the end of § 34.)—Eds.]

are generally enlarged at regular intervals, so that they appear to consist of a series of many portions, and give a transversely striated aspect to the muscular fibres, or they appear more even, and then the primitive bundles present a longitudinal striation. Besides these fibrils, the muscular fibres contain nothing but a small quantity of the viscid substance uniting them, and a certain number of rounded or elongated cell-nuclei, which generally lie against the inner surface of the *sarcolemma.* The association of the muscular fibres into muscles and muscular membranes occurs in such a manner that they either apply themselves parallel to one another, or are united into true networks of transversely striated muscles. They then receive an investment of more delicate or firmer connective tissue, the so-called *perimysium,* with which finer elastic fibres and also fat-cells are frequently mingled; and are, besides, surrounded by numerous blood-vessels and nerves.

Fig. 35.

Fig. 36.



In chemical characters the principal substance of the transversely striated muscular fibres agrees perfectly with the *syntonin* referred to in the previous section. The *sarcolemma* is very resistant to acids and alkalies, whilst the nuclei present the common characters of those organs. A fluid with an acid reaction may be expressed from the muscles, in which Liebig and Scherer have discovered an interesting series of non-

Fig. 35. Two muscular fibres of man, × 350. In the one the bundle of fibrils, *b*, is torn, and the sarcolemma, *a*, is to be seen as a mere empty tube.

Fig. 36. Primitive fibrils from a primitive bundle of the Axolotl (*Siredon pisciformis*); *a*, a small bundle of them; *b*, an isolated fibril, × 600.

nitrogenous and nitrogenous products of the decomposition of the muscular tissue.

The transversely striated muscles are in a high degree contractile, and are the chief instruments of the animal motions. Their elements are developed by the coalescence of round or stellate cells, whose contents change into a homogeneous, semi-fluid substance, and then break up into fibrils. Once formed, the muscular fibres grow by the elongation and thickening of their elements, and in their complete condition they enjoy a very energetic nutrition, which is especially manifested by the multiform products of their decomposition, as well as by the circumstance that their powers are exhausted in a short time when the circulation is suspended. Wounds of the muscles never heal by transversely striated muscular substance; but an adventitious formation of this tissue appears to occur sometimes, though rarely.

Transversely striated muscular tissue is found in the following parts:

1. In the *muscles of the trunk and extremities; of the globe of the eye*, and *in all those of the ear.*

2. In the *muscles of many organs;* as the *larynx, pharynx*, tongue, and œsophagus (upper half), the end of the *rectum* (*sphincter externus, levator ani*), the genital organs (*bulbo-ischio-cavernosus, urethralis transversus, transversi perinæi, cremaster*, muscular fibres of the round ligaments of the uterus, in part.

3. In *certain parts of the vascular System, e. g.* in the heart and in the walls of the great veins which open into it.

[The muscular fibres of animals are not all composed of bundles of transversely striated fibrils, but present a series of other forms, which may best be grouped in the following manner:

1. Muscular tubes, with homogeneous, semi-solid, not transversely striated contents (most Molluscs, Worms, and Radiata).

2. Muscular tubes with a membrane, a semi-fluid, homogeneous, cortical layer in contact with it, and a fluid or granular, frequently transversely striated or nucleated central substance. (Muscles of *Petromyzon* in part, certain muscles [of the lateral line and of the spiracles] of the plagiostome and osseous Fishes. Muscles of the *Hirudinidæ, Lumbricidæ*, of *Paludina* in part, and of *Carinaria*).

3. Similar muscular tubes with a transversely striated cortical layer without distinct fibrils. (Many muscular fibrils of the *Hirudinidæ,* and of the muscles of Fishes enumerated under 2).

4. Muscular fibres without any internal cavity, with a *sarcolemma* and transversely striated contents, which do not break up into fibrils, but frequently into discs (Bowman), *Salpæ,* some Radiata, many Articulata.

5. Similar muscular fibres, which readily break up into fibrils. (Most Vertebrata, certain muscles of Insects).

6. Simple isolated cells, whose contents are changed into a transversely striated substance, which either fills the whole cell or forms only a thin layer upon its membrane. Here my observations lead me to place the peculiar cartilaginous striæ, which Purkinje (Mikr. neurol. Beobachtungen, in Müll. 'Arch.,' 1845) found in the endocardium of Ruminants. They consist of large polygonal cells with beautiful nuclei, which internally, but as it seems only upon their wall, contain a transversely striated substance, which is not distinguishable from that in the muscular fibres.

All these forms are readily comprehended, if the genesis of the true transversely striated muscular fibres in the higher vertebrata be properly understood (see the special part, Muscles); and I cannot agree with the supposition of Stannius (Gött. Nachr., 1851, p. 17), that the transversely striated muscular fibrils are developed according to many, essentially different types. *Even the gap which has hitherto separated the smooth from the transversely striated muscles becomes less,* when we remember that the so-called transversely striated muscular fibrils may also have *homogeneous non-striated contents,* and also that even when transversely striated they may appear as *isolated cells.*[1]

Muscular fibres of the same description as the transversely striated muscles, and in part actually striated, are very widely distributed. In the Vertebrata such muscles are found in the œsophagus of some Mammalia and of the plagiostome fishes, in the intestine of *Tinca chrysitis,* in the stomach of *Cobitis*

[1] [The muscles of the Medusæ consist of flat, fusiform bands, whose ends are interlaced like those of smooth muscle, but which present the most distinct transverse striæ.—Eds.]

fossilis, around the poison gland of Snakes, and in the contractile organ of the pharynx of the Carp; in the skin of Mammalia, Birds, Snakes, and tailless Batrachians (so-called cutaneous muscles), in the tactile hairs of mammals, in the lymph hearts of many Birds and Amphibia; in the auriculo-ventricular valve of the right side in Birds, and the *Ornithorhynchus;* upon the *vena cava inferior* of the Seal, close above the diaphragm; in the interior of the eye of Birds; and round Cowper's and the anal glands of mammals. In the Invertebrata, as we have mentioned, all the muscles belong to this category, whether they be transversely striated or not; and they are found, therefore, in the heart, the intestine, the *genitalia,* and often clearly striated.

The anastomosis of the primitive bundles of the muscles, with which Leeuwenhoek was already acquainted,[1] and which I rediscovered in the heart of the frog, has now been seen in many places, and appears to be constant in the hearts of the lymph and blood-vascular systems of all animals, and in the muscles of the Invertebrata, especially those of the vegetative and generative organs (Hessling, Leydig). Simple arborescent branchings of muscular fibres, which Corti and I noticed in the tongue of the frog, are on the other hand rare, and have been seen elsewhere only in *Artemia salina,* and in the oral and anal discs of *Piscicola* (Leydig).][2]

Literature.—W. Bowman, article Muscle and Muscular Motion, in Todd's 'Cyclopædia of Anatomy,' and 'On the Minute Structure of Voluntary Muscle,' in 'Phil. Trans.,' 1840, II, 1841, I; J. Holst, 'De Structurâ Musculorum in genere et annulatorum Musculis in Specie,' Dorp. 1846; M. Barry, 'Neue Unters. über die schraubenförmige Beschaffenheit der Elementarfasern d. Muskeln, nebst Beobachtungen über die musculös. Natur d. Flimmerhärchen' (Müll. 'Arch.,' 1850, p. 529).

[1] [It has been pointed out to us by Professor Sharpey, that Leeuwenhoek was not acquainted with the anastomosis of the primary bundles of the cardiac muscles, but has described and figured only that of the secondary bundles, which is indeed obvious upon reference to Leeuwenhoek's Plate ('Experimenta et Contemplationes,' Op. Om. Lugd. Bat., tom. i, p. 409, 1722); the ascription in the text is therefore an error. For other remarks upon the muscular tissue, *vide infra,* § Muscle.—Eds.]

[2] [Such branched muscular fibres may be found beautifully marked in the upper lip of the Rat, and in the tongue of Man and Animals. See article 'Tongue,' by Dr. Hyde Salter, in Todd's 'Cyclopædia.'—Eds.]

§ 28.

Nervous Tissue.—The essential elements of this tissue are of two kinds, the *nerve-fibres* and *nerve-cells* (*ganglion globules*). The primitive fibres or tubules of the nerves have either a distinct medulla or they have none. The former consist of three parts; of a structureless delicate membrane, the sheath of the primitive tubules; of a central, soft but elastic fibre, the *central* or *axis-band* (*axis-cylinder*, Purkinje; *primitive band* of Remak); and of a viscid white layer placed between them, the *medullary sheath.* In the tubules without medulla, which in man occur only in certain peripheral expansions (retina, olfactory organ, cornea, Pacinian corpuscles), the structureless coat contains nothing but a homogeneous or finely granular, clear substance, which appears to be identical with the central band of the other tubules, and at any rate may be considered analogous to it, so that the medullary layer may be supposed to be absent in these. The primitive nerve tubules of both kinds, especially of the former, occur of very different dimensions, and may thence be divided into fine ones of 0·0005—0·002‴, those of a medium size of 0·002—0·004‴, and thick ones of 0·004—0·01‴. Their course is either isolated, so that one tubule runs from the centre to the periphery; or they divide, especially in their terminal expansions, into a greater or smaller number of branches; or, lastly, they form actual anastomoses and networks. Besides this, many nerve-tubules are connected with nerve-cells, so that they either arise from them or are interrupted in their course by interposed nerve-cells. These nerve-cells, or as they are called in the ganglia,

Fig. 37.

Fig. 37. Tubular nerve-fibres of man, × 350. Four of them fine, two of them being varicose, one of a medium thickness with a simple contour, and four thick ones; two having double contours, and two with granular contents.

Fig. 38.

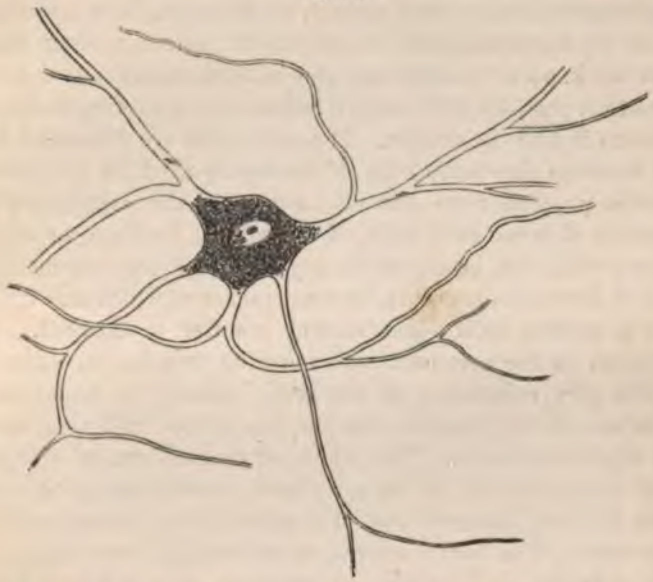
ganglion-cells or *ganglion-globules*, are endowed with the common attributes of cells. Their membrane presents no peculiarity, except that, frequently, it is very delicate, and even, as in the great central masses, eventually perhaps wholly disappears. The contents are finely granulated, semi-solid, often contain pigment, and without exception inclose a distinct vesicular nucleus with a large nucleolus. In size, the nerve-cells vary from 0·003—0·04‴, and as regards their form, they may be distinguished principally into round, fusiform, and stellate. The two latter kinds are produced by the prolongation of many nerve-cells into two, three, to eight and more, processes, which in some cases, after a short course, pass into medullated nerve-fibres, in others, present a more marked independence, since, preserving a complete resemblance to non-medullated nerves, they often run for a considerable distance, and branch out in manifold ways. In what manner finally these processes end, whether free or in connection with nerve-tubules or by anastomosis with similar processes, is not yet made out; though, upon the whole, it would seem to be not improbable that all three possibilities may occur in different localities.

Nerve-fibres and nerve-cells are combined into two substances, which in extreme cases present very wide differences, the *grey* and the *white* substances. The former constitutes the so-called white medulla or medullary substance of the spinal cord and brain, and the nerves; it consists essentially of nerve-tubules, united into bundles or interwoven into plexuses, with blood-vessels; added to which, in the peripheral nerves, we have special investments of connective tissue, the so-called

Fig. 38. Nerve-cell of the Pike (so-called *bipolar*), passing at its two ends into dark-bordered nervous tubules, treated with arsenious acid, × 350: *a*, membrane of the cell; *b*, nerve-sheaths; *c*, medulla of the nerve; *d*, axis-fibres connected with the contents of the nerve-cell; *e*, retracted from the membrane.

neurilemma. The *grey substance* contains a great preponderance of nerve-cells, besides which, in certain localities, there is a finely granular matrix and free nuclei; but it is rarely found quite unmixed, being usually mingled more or less with nerve-

Fig. 39.



fibres. This is more especially the case in most ganglia, in the grey substance of the spinal cord, and in the so-called ganglia of the cerebrum; while on the other hand, in the grey cortex of the cerebrum and cerebellum, it is found in some localities almost without nervous fibres. This substance possesses vessels even in much greater abundance than the white; and in the peripheral ganglia there are also different forms of connective tissue, which serve to invest their separate parts.

The chemical composition of the nervous substance has hitherto, by no means, been sufficiently investigated. In the white substance, the central bands of the nerve-tubules consist of a protein compound very similar to the fibrin of the muscles; the medullary sheath, chiefly of fats of different kinds, and the membrane, of a substance similar to the sarcolemma. The grey

Fig. 39. Nerve-cells of the *substantia ferruginea* from the floor of the fourth ventricle in man, × 350.

substance contains a preponderance of albuminous matter, besides a considerable quantity of fat.

The *physiological* importance of the nervous tissue consists, in the first place, in its subserving movement and sensation; secondly, in its exerting a certain influence upon the vegetative functions; and thirdly, in its serving as a substratum to the psychical activities; in all which capacities, according to what we know at present, the grey substance performs the more important part, the white acting rather as a connecting conductor between it and the organs. The nerve-cells are developed from the common formative cells of the embryo, whilst the nervous tubules proceed from the coalescence of the membrane and contents of many such cells, of a rounded, fusiform, or stellate shape; with this, in the medullary tubules a peculiar modification of the contents occurs, in consequence of which it is divided into a central solid filament and a softer investment. The nutrition in the nervous tissue must be very active, especially in the grey substance, as the great quantity of blood which flows into it clearly shows, but the products of its decomposition are wholly unknown. The white nervous substance is regenerated pretty readily in the peripheral nerves, and as it would seem, in the spinal cord also. The adventitious formation of nervous tubules has been observed in pathological, new formations, and according to Virchow's observations, it would even appear that an abnormal development of grey substance may occur.

The organs composed of nervous substance are: the peripheral nerve-cords, nerve-membranes and nerve-tubules, the ganglia, the spinal cord, and the brain.

[Medullated nerve-fibres are found only in the Vertebrata, and even in that class not in every division, as for example, in *Petromyzon* (Stannius). Fibres without medulla always occur together with the former, and in general in the same localities as in man; but in other situations also, as in the skin of the Mammalia, in the electric organs of Fishes, and in the sympathetic nerve of the Plagiostomata (Leydig). Where nerves are found in the Invertebrata, they contain only pale fibres without medulla, whose structure often completely resembles that of the embryonic fibres of higher animals, especially as regards the occurrence of great nucleated enlargements in the terminal ex-

pansions, which remains of the original formative cells, have, recently, less properly been considered to be ganglion-globules.]

Literature.—G. Valentin, 'On the course and termination of the nerves,' in the 'Nov. Act. Natur. Curios.,' vol. xviii, t. i; R. Remak, 'Observations anatomicæ et microscop. de syst. nerv. struct.,' Berol., 1838; A. Hannover, 'Recherches microscopiques sur le système nerveux,' Copenhague, 1844; R. Wagner, 'Neue Unters. über den Bau und die Endigungen der Nerven und die Structur der Ganglien,' Leipzig, 1847; and 'Neurologische Untersuchungen,' in 'Göttingen Anzeige,' 1850; Bidder and Reichert, 'Zur Lehre vom Verhältniss der Ganglienkörper zu den Nervenfasern,' Leipzig, 1847; Ch. Robin, in 'l'Institut.,' 1846, Nos. 687—699, and 1848, No. 733; Kölliker, 'Neurologische Bemerkungen,' in 'Zeitsch. für wiss. Zool.,' i, p. 135.

§ 29.

True Glandular Tissue.—The most essential constituents of the true glands are the *secreting elements,* which appear as aggregations of cells, as closed glandular vesicles, and as open glandular vesicles and glandular tubes, containing as their most important constituent the so-called *gland-cells.* These cells are for the most part polygonal or cylindrical, and perfectly resemble certain epithelial cells, but upon the other hand, they are frequently distinguished and characterised by peculiar contents. The union of these cells into the secreting parts of the glands is effected either directly or with the cooperation of homogeneous membranes, the so-called *membranæ propriæ,* and of connective tissue. In this manner the secreting glandular elements, different in nature according to the different glands, are formed; and becoming invested with vessels, nerves, and connective tissue, with which elastic fibres, fat cells, and even muscles, are mingled; they are combined into the larger and smaller divisions of the glands. The principal forms of the secreting glandular elements in man are the following:

1. *Solid networks of cells without investing membrane.* In the liver (fig. 40).

2. *Closed vesicles with a fibrous membrane and an epithelium.* Graafian vesicles, mucous follicles (so-called *ovula Nabothi*), in the *cervix uteri.*

3. *Rounded or elongated glandular vesicles, with a membrana propria and an epithelium.* In the racemose glands (fig. 41).

4. *Glandular tubes, with a membrana propria, or a fibrous membrane and an epithelium.* Tubular glands (fig. 42).

Fig. 40.

Fig. 41.

To these elements are also added, (except in those glands enumerated under 2, which become emptied of their contents by the occasional bursting of their follicles, and the simplest tubular glands) special excretory ducts, which, after manifold ramifications, either pass directly into the glandular vesicles and glandular tubes, or, as in the liver, are simply applied to the secreting networks of cells. These ducts are at first similar in their structure to the secreting parts, but they always possess epithelial cells, which have not the specific contents of the proper gland cells, and mostly also exhibit a different form. The wider excretory ducts consist of a fibrous investment and of an epithelium, and often also, possess a muscular layer, and in their ultimate divisions, a fibrous, a muscular and a mucous layer very frequently exist as special structures.

Chemically, the glands are, as yet, little known. The glandular cells, as the most important structures, are allied in this respect also, to the epithelial structures, only that frequently,

Fig. 40. Network of hepatic cells, *b;* and finest *ductus interlobulares, a;* of man after nature; the union of both diagrammatic, × 350; *c*, vascular spaces.

Fig. 41. Two of the smallest lobes of the lung, *aa;* with air-cells, *bb;* and the finest bronchial ramifications, *cc;* upon which also air-cells are seated. From a new-born child, × 25; semi-diagrammatic figure.

they contain in their interior peculiar substances,—as fat, the constituents of the bile, of the urine, of the gastric juice, mucus, &c., and thence assume a specific character.

Fig. 42.

The true glands either separate certain constituents from the blood, or by means of it, elaborate peculiar substances or structural elements, and according as they do the one or the other, is the import of their separate parts different. In the former glands the cells play a more subordinate part, and are at most of importance, so far merely, as they impede the passage of this or that constituent of the blood, and allow only certain of them to pass (kidneys, lachrymal glands, small sudoriparous glands, lungs); whilst in others, the cells take a very important share in the formation of the glandular fluid, by producing within them the specific secretion, which then either drains out of them (liver, mucous glands, gastric glands, prostate, Cowper's glands, salivary glands, pancreas), or becomes free by the gradual dissolution and breaking-up of the cells themselves (lacteal glands, fat-glands, testis, larger sudoriparous and ceruminous glands). In the former case, as in the Graafian follicles, a peculiar cell-development may take place in the secretion which is formed, whilst in the latter, new elements continually arise in place of those gland-cells which are removed as they attain their full development, in consequence of which the character of these cells as a coating of the glandular canals is frequently lost, and they appear simply as a part of the secretion (*testis*, lacteal gland during lactation). All the glands here mentioned, with the exception of the sexual, are developed from the internal and external epithelial structures of the body, conjoined with the vascular membranes which support these epithelia. Some of them originate as involutions of these membranes, and retain the cavities throughout the course of their deve-

Fig. 42. Gastric gland from the *pylorus* of the dog, with cylinder-epithelium: *a*, larger glandular cavity; *b*, tubular appendages of it.

lopment (lungs, small intestinal glands), others are at first hollow, but afterwards increase by the addition of solid outgrowths (liver); others, again, are solid from the very first, continue to grow in this condition, and only secondarily come to possess cavities (cutaneous glands, racemose glands). The nutrition of the glands goes on with great energy, and they belong to the most vascular organs of the body. Except in the uterine glands, no regeneration of the glandular substance takes place, but hypertrophy occurs in them, and even the accidental formation of minute glands.

The true glands of the human body may, according to the form of their ultimate elements, above described, be divided as follows:

1. *Glands with closed glandular vesicles,* which dehisce periodically. Ovary, follicles of the uterus.

2. *Glands whose parenchyma consists of cells united into a network.* Liver.

3. *Racemose glands,* in which, rounded and elongated glandular vesicles are seated upon the ultimate ends of the excretory ducts.

a. simple, with one or few glandular lobules. Mucous glands, sebaceous glands, Meibomian glands.

b. composite, with many glandular lobules. Lachrymal glands, salivary glands, pancreas, prostate, Cowper's and Bartholini's glands, lacteal glands, lungs.

4. *Tubular glands,* whose secreting elements have the form of canals.

a. simple, consisting of only one or a few cæcal tubes. Tubular glands of the stomach and intestine, uterine glands, sudoriparous and ceruminous glands.

b. composite, with many branched glandular canals, which may also be united into a network. *Testis,* kidney.

[The forms of the glands of animals, notwithstanding their variety, may, with few exceptions, be brought under one of the four categories here established. The following are worthy of particular notice: 1. The glandular cells, with peculiar excretory ducts, to be found in some Articulata, which either, singly, form glands, or are united together in numbers by a *membrana propria.* 2. The occurrence of a structureless, chitinous *membrana intima* in many glands of the Articulata. 3. The formation of

certain secretions [*Uric acid* and *bilin* in Mollusks, *bilin* in Crustacea] within special spontaneously enlarging "secreting vesicles" (Nägeli, H. Meckel), which may be compared to the yelk vesicles (§ 6). 4. The colossal size (up to 0·1‴) of many glandular cells of Insects, and the peculiar ramifications of their nuclei.]

Literature.—J. Müller, 'De Glandularum secernentium structurâ penitiori,' Lips. 1830; H. Meckel, 'Micrographie einiger Drüsenapparate niederer Thiere,' in Müll. 'Arch.,' 1846; Fr. Leydig's 'Vergleichend-anatomische Abhandlungen,' in 'Zeitschrift für wiss. Zool.'

§ 30.

Tissue of the Blood-vascular Glands.—Under this denomination are most appropriately comprised, a series of organs, which agree in this, that in a peculiar glandular structure, they elaborate from the blood or other juices certain substances which are not excreted by special, permanent, or periodically-formed excretory ducts, but simply by filtration from the tissue, and are afterwards applied in one way or another to the general purposes of the organism.

It may be, that this wide definition includes organs, which it will be necessary to separate in future; but with our present slight knowledge of these structures, it is the only one which is possible without entering more fully into the subject.

The essential glandular tissue of the organs in question appears under the following forms:

1. *As a parenchyma of larger and smaller cells*, imbedded in a stroma of connective tissue. *Supra-renal bodies, anterior lobes of the hypophysis cerebri.* Some of the cells

Fig. 43.

Fig. 43. A few of the glandular vesicles from the thyroid gland of a child, × 250: *a*, connective tissue between them; *b*, membrane of the glandular vesicles; *c*, their epithelium.

here attain the great size of 0·04‴; and then contain, together with a granular substance, many nuclei, and perhaps secondary cells.

2. *As closed follicles*, each of which consists of a *membrana propria* with an epithelium upon its inner side, and has clear contents: *thyroidea*. The follicles, which are not enlarged cells, are surrounded by a large quantity of connective tissue, and are united by it into smaller and larger lobules.

3. *As closed follicles*, with a membrane of connective tissue, and contents consisting of nuclei, cells and some fluid. Among these I enumerate:

a. The solitary follicles of the stomach and intestine; and

b. The aggregated follicles of the small intestine, or Peyer's patches (in animals those of the stomach and large intestine also), both of which contain numerous blood-vessels in the interior of the follicles.

c. The follicular glands in the root of the tongue, the tonsils, and the pharyngeal follicles, which in the walls of their sacs, contain many closed follicles like those above mentioned, but, so far as we as yet know, without vessels in their interior.

d. The lymphatic glands, which appear to consist of follicles like those of the Peyerian patches.

4. *As a cellular parenchyma, which contains numerous closed follicles* like those just described: Spleen.

Fig. 44.

5. *As racemose, aggregated, glandular vesicles opening into a common closed canal or broad space*, whose thick walls are formed of a delicate investment of connective tissue, and of a soft substance consisting of many nuclei and of vessels: Thymus.

We know little of the chemical nature of these organs, which are all more or less richly supplied with blood-vessels. Those enumerated under 1, 2, 3, and 5, contain much protein and fat in their tissue, as also do the

Fig. 44. A Malpighian corpuscle from the spleen of the ox, × 150: *a*, wall of the corpuscle; *b*, contents; *c*, wall of the artery upon which it is seated; *d*, sheath of the latter.

follicles of those included under the fourth form, while the remaining parenchyma of the spleen possesses peculiar corpuscles, not yet completely investigated, which seem to indicate an energetic, retrogressive metamorphosis. We know little of the physiological functions of these glands; and here it need merely be remarked, that in the spleen, the thyroid, the thymus, the supra-renal capsules, and the pituitary body, it can only be the blood which yields material to them, and only the blood- and lymph-vessels which again receive the substances given off externally or internally (thymus) by them. In the follicular glands of the mouth and pharynx, the secretions are poured into the wider cavities of the glands, and ultimately into those organs, whilst in the intestinal follicles, it is doubtful whether they excrete substances into the intestine, or receive them from thence to give them up again to the vessels. In the lymphatic glands, the ducts supply the glandular follicles with matters which they take up again when further elaborated.

The development of the blood-vascular glands is still very obscure; although this much appears certain, that most of them are developed without the participation of the intestinal epithelium, either from the fibrous wall of the intestine or from the same blastema as that which produces the sexual glands. The thymus and thyroid alone are to be regarded, according to Remak, as diverticula of the intestinal canal.

The *nutrition* of most of these glandular structures is very energetic, as the abundance of the blood they contain and their frequent morbid alterations show: the *hypophysis cerebri* and the supra-renal capsules alone, in this respect, occupy a lower grade.

Literature.—A. Ecker, art. 'Blood-vascular Glands,' in 'Wagner's Handw. d. Phys.', Bd. IV, 1849. [H. Gray, 'On the Development of the Ductless Glands in the Chick,' Philosoph. Trans., 1852.—Eds.]

SPECIAL HISTOLOGY.

OF THE EXTERNAL INTEGUMENT.

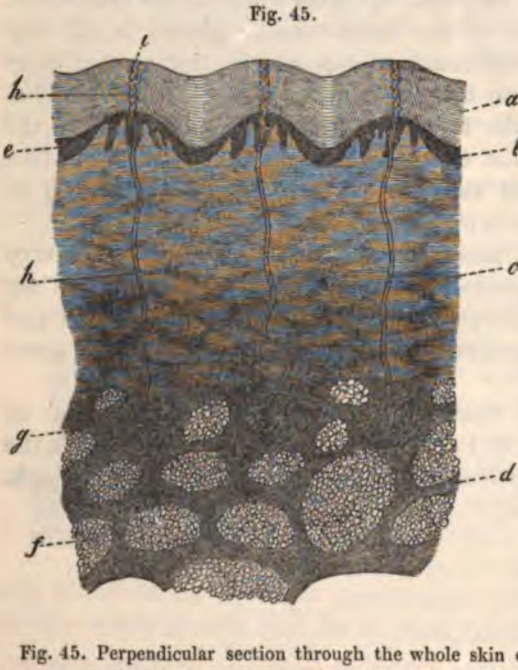
I.—OF THE SKIN IN THE STRICTER SENSE.

A. CUTIS.

§ 31.

The external skin, Integumentum commune (fig. 45), consists essentially of an internal layer formed principally of connective tissue, and rich in vessels and nerves, the true skin, *cutis, derma* (fig. 45, *c*, *d*); and of an external layer composed of cells only, the *epidermis* (fig. 45, *a*, *b*); and it contains in addition many peculiar, glandular and horny organs.

Fig. 45.



The *cutis* may be again subdivided into two layers, the subcutaneous cellular tissue, *tela*

Fig. 45. Perpendicular section through the whole skin of the ball of the thumb, transversely through three ridges of the cutis, × 20 : *a*, horny layer of the epidermis; *b*, its mucous layer; *c*, *corium; d*, *panniculus adiposus* (upper part); *e*, papillæ of the cutis; *f*, fat masses; *g*, sudoriparous glands; *h*, their canals; *i*, sweat-pores.

cellulosa subcutanea (fig. 45, *d*), and the proper *corium* (fig. 45, *c*); the latter of which, from its rich nervous and vascular supply, forms the most important part of the skin.

§ 32.

The *subcutaneous cellular tissue* is a tolerably firm membrane, constituted chiefly of connective tissue, which in by far the most parts of the body, incloses within its meshes a considerable quantity of fat-cells (fig. 45, *f*), thus forming the *panniculus adiposus;* in some situations, however, as for example in the *scrotum,* the *penis,* and the *nymphæ,* &c., it contains but little or even no fat. The innermost layer of the subcutaneous cellular tissue, which upon the trunk and thighs forms a tolerably firm fatless texture, the *fascia superficialis,* rests upon different organs, as muscular *fasciæ, periosteum* and *perichondrium,* muscles, and the deeper accumulations of fat, and is more or less closely united with them. The union is looser upon the trunk, the two distal divisions of the limbs, the back of the hand and foot, the neck, and especially on the eyelids; the penis, scrotum, and on the extensor side of the articulations, where the subcutaneous mucous *bursæ,* as they are called, are frequently situated, as, for instance, in the knee, elbow, and phalangeal joints. A more close connection sometimes exists, — as where tendinous fibres or processes (*aponeurosis palmaris* and *plantaris, linea alba*), or muscles (*palmaris brevis, levator labii superioris alæque nasi, levator labii superioris,* &c.), are inserted into the skin; sometimes,—as where the innermost layers of the subcutaneous cellular tissue are blended, as it were, by means of short, strong, filaments of connective tissue with the subjacent muscles, *fasciæ,* tendons, &c. particularly, therefore, on the head, especially on the *alæ nasi* and lips, the forehead and temples, the ear, mouth, and occiput; on the *glans penis,* beneath the nails, &c. In general, where the fat forms a thick layer, the skin is less moveable than when from any cause it is less abundant or entirely absent.

The external surface of the subcutaneous cellular tissue, is connected by means of numerous filamentary processes of connective tissue, with the *corium,* and is not everywhere clearly distinct from it; but a separation between the subcutaneous cellular tissue and the *corium* may be pretty readily

effected, especially when the former contains an abundance of fat, with the exception of certain situations (head, cheeks, chin, &c.), where the follicles of the larger and more closely set hairs penetrate deeply into the *panniculus adiposus.* The subcutaneous cellular tissue of the *penis, scrotum* (*dartos*), &c. passes into the *corium* without any distinct limitation.

The thickness of the subcutaneous cellular tissue varies very considerably, as is well known, according to situation, age, sex, and the individual. The fat-less subcutaneous cellular tissue of the eyelids, and of the upper and outer part of the ear, measures, according to Krause $\frac{1}{4}'''$, on the *penis* $\frac{1}{3}'''$, on the *scrotum* $\frac{2}{3}'''$. The *panniculus adiposus* is 1''' thick on the cranium, brow, nose, lobe of the ear, neck, dorsum of the hand and foot, the knee and elbow; in most other situations it is 2 to 6''', though in fat persons it may exceed 1'' in thickness, and in thin ones may sink below 1'''.

§ 33.

The proper *corium* is a tough, slightly-elastic membrane, and is composed principally of connective tissue, which in the thicker parts presents two, though not very well-defined layers, which may be designated the "reticular" and the "papillary" portions (*p. reticularis* and *p. papillaris*). The former constitutes the inner layer of the *corium*, and consists of a white, reticulated membrane, frequently distinctly laminated in its deeper portions, and containing in special, narrow or wide, scanty or numerous meshes, the hair follicles and cutaneous glands, together with much fat. The papillary part of the *corium* is the reddish-grey external superficial layer (fig. 45), which in its dense, firm tissue, contains the upper portion of the hair-follicles and cutaneous glands, and the terminal expansions of the vessels and nerves of the skin. Its most important element consists in the cutaneous or tactile papillæ, *papillæ tactûs* (fig. 46); small, semi-transparent, flexible, but tolerably solid elevations of the external surface of the *corium*, which are ordinarily conical or clavate in form, but in certain places present numerous points (compound *papillæ*). With regard to their number and position, the *papillæ* of the bed of the nail, of the palm of the hand, and of the sole of the foot, are very numerous (E. H. Weber enumerates upon

Fig. 46.

1‴ square of the *vola manus*, 81 compound, or 150 to 200 smaller *papillæ*), and disposed with tolerable regularity in two principal series, each of which has 2 to 5 papillæ in the transverse direction, placed upon linear elevations, $\frac{1}{10}$ to $\frac{1}{3}$‴ broad, by $\frac{1}{20}$ to $\frac{1}{6}$‴ high,—the ridges of the *corium*. The course of these ridges is visible, even externally in the epidermis, and therefore needs no further description. Elsewhere the *papillæ* are more irregularly scattered, either very close together, as in the *labia minora*, the *clitoris*, the *penis*, and the nipple, or somewhat more widely apart, as upon the extremities, with the exception of the places named, on the scrotum, the neck, chest, abdomen, and back.

Fig. 47.

The size of the *papillæ* varies considerably; the shortest, $\frac{1}{66}$ to $\frac{1}{40}$‴, occur in the face, especially upon the eyelids, brow, nose, cheeks, and chin, where they are even wholly wanting, or are replaced by a network of depressed ridges; next upon the

Fig. 46. Compound papillæ of the surface of the hand, with two, three, and four points, × 60: *a*, base of a papillæ; *bb*, their separate processes; *cc*, processes of papillæ whose base is not visible.

Fig. 47. Horizontal section of the skin of the heel through the apices of the papillæ of one entire and two half ridges, × 60. The serial arrangement of the papillæ corresponding with the ridges of the cutis, is obvious. *a*, Horny layer of the epidermis between the ridges, which from their undulating course are cut through in making a section through the points of the papillæ. *b*, *stratum Malpighii* of the epidermis. *c*, Papillæ which are placed in more than two rows; since, however, many of them are always seated upon a common base, there are, so to say, only two rows of compound papillæ present. *d*, *stratum Malpighii* between the papillæ belonging to a common base, which, because it has a less thickness, here appears somewhat clearer. *e*, Sweat canals.

female breast ($\frac{1}{80}$ to $\frac{1}{60}'''$), upon the scrotum, and at the base of the penis ($\frac{1}{66}$ to $\frac{1}{40}'''$). In most other situations their length is from $\frac{1}{22}$ to $\frac{1}{30}'''$. The longest, $\frac{1}{20}$ to $\frac{1}{30}'''$, exist on the surface of the palm of the hand, sole of the foot, and the nipple, where they are generally of the compound kind; further, the anterior and posterior extremities of the bed of the nail ($\frac{1}{14}$ to $\frac{1}{10}'''$), and the *labia minora* ($\frac{1}{30}$ to $\frac{1}{10}'''$). The breadth at the base in most of the papillæ about equals, or is somewhat less than, the length; in a few, as in those of the scrotum, prepuce, and root of the penis, it even exceeds the length by $\frac{1}{3}$ or more, whence these papillæ exactly resemble warts, or even short ridges; in the longest papillæ, lastly, the breadth is $\frac{1}{3}$ to $\frac{1}{2}$ the length.

The thickness of the *corium* varies from $\frac{1}{8}$ to $1\frac{1}{2}'''$, and in most places is about $\frac{1}{4}$ to $\frac{3}{4}'''$. It is thinnest ($\frac{1}{5}$ to $\frac{1}{8}'''$) in the *meatus auditorius externus*, in the eyelids, the red border of the lip, the *glans penis* and *clitoridis*; and thickest $\frac{1}{2}$ to $1'''$ on the back, chin, upper and lower lip (the hairy part), the *alæ nasi*, upon the ball of the sole, the extremity of the great toe, the *scapula* and the *nates*; on the heel, 1 to $1\frac{1}{2}'''$.

The principal chemical characters of the *corium* agree with those of the connective tissue, of which it is principally constituted. It putrefies with difficulty, and not at all when tanned; it may be easily dried, and then becomes yellowish, transparent, and hard, but flexible and no longer subject to putrefaction. In boiling water, it at first shrinks, eventually however dissolving, but not with equal facility in all animals, and in the young, more quickly than in the old, into gelatine, *colla;* and the same change is effected at the ordinary temperatures, when it is treated with dilute acids and alkalies.

§ 34.

The *corium* is principally composed of connective and elastic tissue, containing in addition, smooth muscles, fat-cells, blood-vessels, nerves, and lymphatics, in great abundance.

The connective tissue consists of the ordinary bundles, which are in part united into a network, as in the subcutaneous cellular tissue; in part into larger secondary bundles, *trabeculæ* and *laminæ*, which, in the *panniculus adiposus*, circumscribe larger and smaller spaces filled with fat; whilst in the *fascia*

superficialis, and in the *corium,* their connection is very intimate, and they form, especially in the latter, a very dense tissue, with indications of lamination. In the *papillæ* the fibrous structure is not everywhere distinct, and instead of it there often exists a more homogeneous tissue,[1] which frequently appears to be bounded by a structure-

Fig. 48.

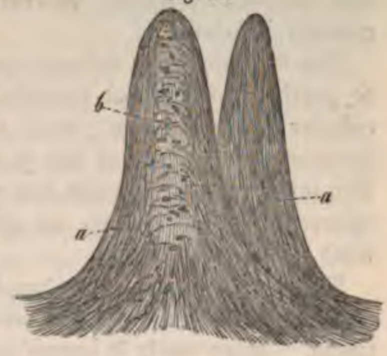


Fig. 49.

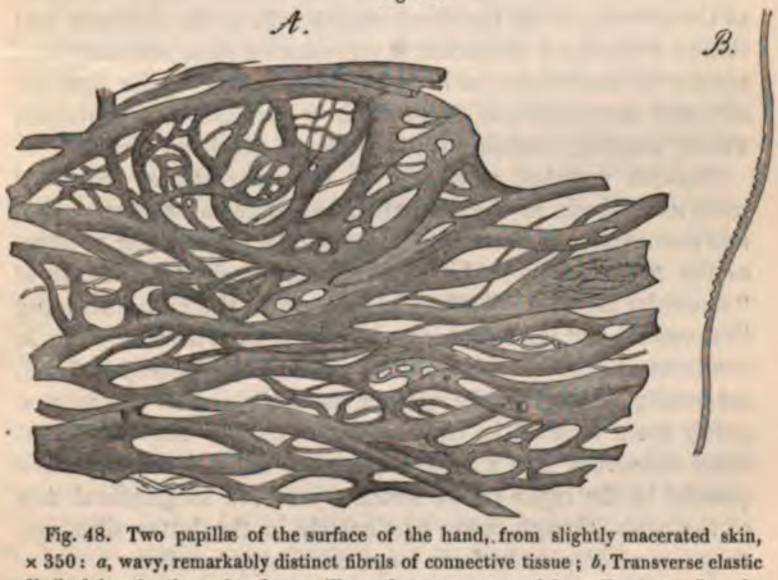


Fig. 48. Two papillæ of the surface of the hand, from slightly macerated skin, × 350: *a*, wavy, remarkably distinct fibrils of connective tissue; *b*, Transverse elastic fibrils lying in the axis of a papilla and transverse nuclei, *axile corpuscles*, the *corpuscula tactûs* of R. Wagner (see § 37); of nerves no trace is to be seen without reagents.

Fig. 49. *A*, Elastic fibres from the inner part of the *fascia lata* of man, closely interwoven, and appearing like an elastic membrane, × 450. *B*, An elastic fibre with a serrated edge, such as may also be seen occasionally in the cutis.

[1] [The most superficial layer of the cutis is invariably composed of a transparent matrix, homogeneous or nearly so, in which nuclei are imbedded. The "indications of lamination" are simply the commencement of the breaking up of this tissue into areolated connective tissue, such as we have already described; see note, p. 83. —Eds.]

less membrane, which, however, does not admit of being actually isolated.

The *bursæ mucosæ subcutaneæ* are nothing but larger, simple, or partially subdivided reticular spaces, in the subcutaneous cellular tissue, in the *fascia superficialis* (*bursa olecranii*), or between the laminæ of the *fascia muscularis* (*bursa patellæ*). The internal walls, smooth but uneven, are formed of common connective tissue, possess no epithelium, and include a somewhat viscid, clear fluid.

The elastic tissue exists abundantly in almost all parts of the cutis; but, in general, far more sparingly than the connective tissue. More rarely it occurs in the form of true elastic membranes, which may even resemble the densest elastic networks of the arteries, as in the *fascia superficialis* of the abdomen and thigh; while more commonly it represents a loose reticulation of coarser or finer fibres, as in the *corium*. The *papillæ* (but not all), and the *panniculus adiposus*, in which they are sometimes wholly wanting, contain only fine elastic (nucleus) fibres.

Smooth muscles, according to my observations, occur far more extensively in the skin than has hitherto been supposed, and particularly in the *subcutaneous cellular tissue* of the *scrotum*, or the *tunica dartos*, which has thence received the name of "muscular membrane" (Fleischhaut), and of the *penis*, including the prepuce and the anterior part of its body, where they run in the form of yellow bundles (whose elements are figured in § 26), measuring $\frac{1}{3}'''$ to $\frac{1}{4}'''$ partly contiguous to the vessels and nerves, partly more isolated in the connective tissue; they are sometimes converted into a network, but are more usually disposed parallel to the raphe of the scrotum and the longitudinal axis of the penis, though, more particularly in the latter situation, they not unfrequently form large transverse bundles.

2. In the *areola* of the nipple, the smooth muscles, which are especially well developed in the female, are disposed circularly in a delicate layer, which becomes thicker internally towards the base of the nipple, and are, for the most part, visible to the naked eye, on account of their yellowish red colour, and the thickness of their bundles (up to $\frac{1}{3}'''$); in the nipple itself they run in part circularly, in part perpendicularly, and are united into a close network, through whose meshes the excretory ducts of the lacteal glands pass.

3. Lastly, smooth muscles are also found in the superficial portions of the *corium*, and in fact, in all situations where hairs occur, in the form of flat bundles, 0·1—0·16‴ broad, which, singly or in pairs, are invariably placed near the upper part of the hair follicles and sebaceous glands. They arise, probably, from the superficial part of the *corium*, and running obliquely from without inwards, towards the hair-follicles, surround the sebaceous glands, and are inserted close behind, and near the base of those glands into the hair-follicles.

[Quite recently Eylandt and Henle have added to our knowledge of the smooth muscles of the skin. The existence of the little muscles of the hair follicles, termed by Eylandt, *arrectores pili*, has been confirmed by both writers, only that they find them to be more delicate (Eylandt 0·02‴, Henle 0·04‴). Eylandt never noticed more than one bundle passing to a hair follicle, and Henle states that they sub-divide upwards into many bundles of 0·004‴, and may be traced immediately under the *epidermis* as far as the papillæ. In the *scrotum*, in the skin of the *penis*, the *perinæum*, the *areola mammæ*, and in the nipple, Eylandt could not find smooth muscles; and he imagines that I have confounded the circular muscles of the vessels with them, a supposition which I should not have allowed myself to entertain even against a beginner. Henle has seen the smooth muscles in all these situations, which it is, in fact, very easy to do, though I think that he goes to the other extreme in assuming the existence of smooth muscular fasciculi in the hairless portions of the skin also, in the sudoriparous glands, and in the vascular ramuscules (on their exterior), and, I believe, that in these cases, he has been misled by fine nervous twigs, which, as he himself states, may readily be confounded with smooth muscles, in the boiled preparations which he employed.]

§ 35.

Fat-Cells.—These cells are especially developed in the *panniculus adiposus*. In this situation the fat-cells do not form large continuous expansions, but occupy, in larger or smaller clusters, the variously formed meshes of the connective tissue (fig. 45 f). Each of the yellow clusters, or fat-lobules, which appear to the naked eye clearly defined, has a special coating of connective tissue, in which the vessels intended for the

nutrition of the fat-cells are distributed, and consists either of a simple aggregation of cells, or of a number, varying according to its size, of smaller and smallest lobules, each of which again has its proper delicate investment of connective tissue. According to Todd and Bowman, every cell even, has its own special covering and vessels; but this, though true in many cases, is certainly not so in all. In the *corium* the fat-cells are found more in the deeper part round the hair follicles and sebaceous glands, while they are wholly wanting in the *pars papillaris*. In persons in tolerably good condition, the fat-cells are always rounded or oval 0·01—0·06‴ in diameter, with a dark border, filled with fluid, pale yellow fat, which

Fig. 50.

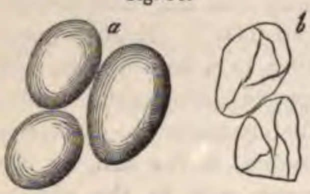


Fig. 51.

forms a single drop—and with a parietal nucleus which is not readily rendered visible (fig. 50). In emaciated subjects, on the other hand, hardly any cells of this kind are met with, but instead, more or less abnormal forms: 1. *Granular cells,* with numerous small fat drops, forming whitish-yellow clustered lobules; 2. *Fat-cells containing serum,* in yellow or reddish-brown minute lobular masses, which, together with the fat (which has become more or less diminished in quantity, and usually appears as a single dark-coloured globule), contain a clear fluid and a distinct nucleus, and are considerably smaller than the normal cells,—0·01—0·015‴; 3. *Cells* which contain *no fat,* but *only serum,* with a distinct nucleus, and having a delicate or thickened membrane; they occur in more gelatinous fatty tissue, or mingled with the others; they are also met with in œdema; 4. Lastly, *Fat-cells containing crystals;* either presenting 1 to 4 stars of acicular crystals (margarin), together with a drop of fat,

Fig. 50. Normal fat-cells from the breast, × 350: *a*, without reagents; *b*, after being treated with ether, whereby the fat is exhausted and the folded delicate membrane remains.

Fig. 51. Fat-cells with crystals of margarin, × 350: *a*, cell with a star of crystalline needles, as they may be found not uncommonly in normal fat; *b*, cell quite filled with crystals, from the white fat-lobules of an emaciated subject.

or being completely filled with crystalline needles. The former occur among other normal cells, the latter only in the white, more isolated, fat-lobules.

[The nuclei in the fat-cells of the adult have not, as far as I am aware, yet been observed, excepting by Bendz (Almind. 'Anat.' p. 122, tab. I, fig. 4), who rarely, very rarely, noticed even two pale nuclei with nucleoli. It is true that Mulder (p. 601), states that they are furnished with one, rarely with two, nuclei, but Donders and Moleschott (*ib.*, p. 602, *et seq.*) upon whom Mulder appears principally to rely, expressly say that they did not detect the nuclei; nor does Donders (in the 'Holländ. Beitr.,' I, pp. 57, 61), say anything about nuclei. I *invariably* find them when the fat has partially disappeared from the cell. In cells completely filled, I first distinctly noticed them, in some cases, in the marrow, and in the fat cells in the muscles; but I do not hesitate in the least to affirm their constant occurrence in all fat-cells, since no one can suppose that they are not formed until after the disappearance of the fatty contents. With respect to what Donders and Moleschott observe, as to the existence of two membranes in the fat-cells, the outer of which is said to be soluble in concentrated acetic acid, and in potass, and the inner not; the former, as Donders himself elsewhere supposes, can be regarded merely as connective tissue, which, in many instances, also penetrates between the separate cells and connects them together, or, probably, is occasionally replaced by a homogeneous connective substance (modified cytoblastema). The crystals in the fat cells are considered by Vögel to be *margarin*. As the forms of *margarin* and *margaric acid* are very similar, the question can be decided only on chemical grounds, and these appear to favour the latter.

The pathological conditions of the fat-cells, although as yet but little investigated, corroborate my assertion of the constant occurrence of the nucleus. Without relying upon Schwann's observation, that the fat-cells of the subcutaneous cellular tissue of a rachitic child a year old, all contained a nucleus, I would more particularly adduce the condition of the fat-cells in cutaneous dropsy. In this affection, as long as the fat in the *panniculus adiposus* has not entirely disappeared, cells con-

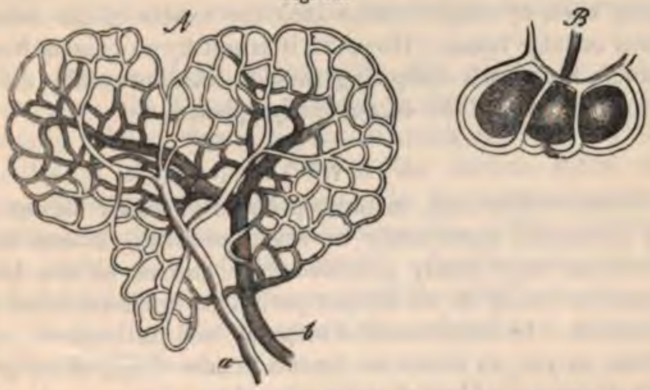
taining serum, and but a small quantity of fat, are extremely abundant, and exactly of the same form as those which are found in emaciated subjects, all with distinct nuclei; and, besides these, there are numerous cells containing nothing but serum and also nucleated. In cases where the fat may be said to have altogether disappeared, and the colourless subcutaneous cellular tissue is infiltrated throughout with water, I find the last-mentioned cells in greatly preponderating quantity, and associated with them, others of peculiar form. In the first place, fusiform or stellate cells, with from three to five irregular, often tolerably long processes, with a distinct nucleus, and mostly only scanty and minute dark fat granules; these, as the very numerous and various transitionary forms indicate, being developed from diminished cells containing serum, and from which the fat has been partially or wholly removed; secondly, roundish or elongated minute (0·003—0·006‴) cells closely filled with dark granules, and without a visible nucleus, which, as is also easy to be perceived, owe their origin to a diminution of the fat-cells coincident with a change in their contents, and, on the other hand, are metamorphosed into the cellules with little or no fat, and containing serum, with which they are found associated. I may also mention that, in the inflamed medulla in the articular ends of the bones, as, according to Hasse, appears to be the case in rheumatism, I have seen the common fat-cells transformed into round and even fusiform cells, containing serum and little fat, and occasionally furnished with nuclei.] (From Kölliker, 'Mikrosk. Anat.,' Bd. II, p. 18.)

§ 36.

Vessels of the Skin.—In the subcutaneous cellular tissue the arteries entering the skin give off many branches to the hair-follicles (see below), the fat-lobules, and the smooth muscles, which, for the most part, form wide-meshed networks of fine capillaries; more rarely, particularly in the fat lobules, the network is closer. More externally they supply the sudoriparous and sebaceous glands (see below), and also form terminal expansions in the inner part of the *corium* (*pars reticularis*), but not many: finally, they penetrate into the outermost part of the papillary layer, and into the *papillæ* themselves, where they terminate in a close network of capil-

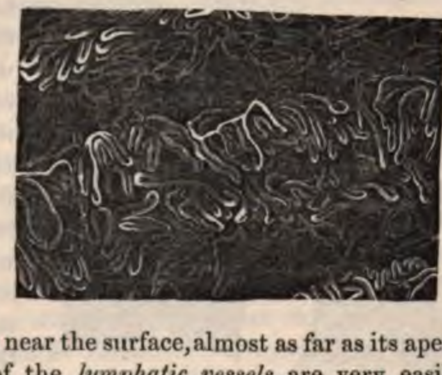
laries with narrow meshes. This consists, wherever there are *papillæ*, of two portions; firstly, of a horizontal plexus lying immediately under the surface covered by the epidermis, and

Fig. 52.



which is composed of larger vessels (of 0·01—0·005''') with wide, and of capillaries (of 0·003—0·005''') with narrow meshes; and secondly, of very many separate loops of the finest vessels (0·003—0·004''') which are given off to the *papillæ*. With certain exceptions (*v.* § 37) every *papilla* possesses its own capillary loop (fig. 53), (the branched *papillæ* have many), which runs, either in the axis of the *papilla* or near the surface, almost as far as its apex.

Fig. 53.



The larger trunks of the *lymphatic vessels* are very easily recognisable in the subcutaneous cellular tissue, and are very numerous. In the *corium* itself different anatomists, Haase, Lauth, Fohmann, &c., have demonstrated the lymphatics by

Fig. 52. Vessels of the fat-cells. *A.* Vessels of a small fat-lobule, × 100: *a*, artery; *b*, vein. *B.* Three fat-cells with their capillaries more magnified; after Todd and Bowman.

Fig. 53. Vessels of the *papillæ* of one entire and two half ridges of the cutis; after Berres.

injecting them with quicksilver. All agree in this, that they form an excessively close network of fine vessels in its outermost part,—according to Krause (l. c., p. 111) of $\frac{1}{15}$ — $\frac{1}{20}'''$ in diameter; the meshes of which become wider internally, and finally open by single trunks into the vessels of the subcutaneous cellular tissue. However, it is not by any means known, whether the vessels composing these plexuses are really the true commencement of the cutaneous lymphatics.

§ 37.

Nerves.—The skin, in those parts of it which border upon the epidermis, particularly in some localities, is one of the structures most richly provided with nerves in the human organism, whilst in its deeper parts it is remarkable for their scantiness. In the *panniculus adiposus*, and in the *fascia superficialis*, as yet, no nerves are known besides those, which giving off a succession of branches, traverse those parts to reach the *corium*, or to supply the hair-glands, smooth muscles, and Pacinian corpuscles, of which we shall speak further on. In the *corium* itself, the trunks which enter through the meshes of the deeper layers ascend by degrees, continually ramifying, but without actually forming, terminal expansions, towards the *pars papillaris*. Here they anastomose frequently, and form rich *terminal plexuses*, in which deeper and more superficial portions may be clearly distinguished, the former consisting of fine branches still containing many primitive tubules, with wide meshes; the second of fibres single or united in pairs, with narrow meshes. In this last or the fine terminal plexus, there also occur

Fig. 54.

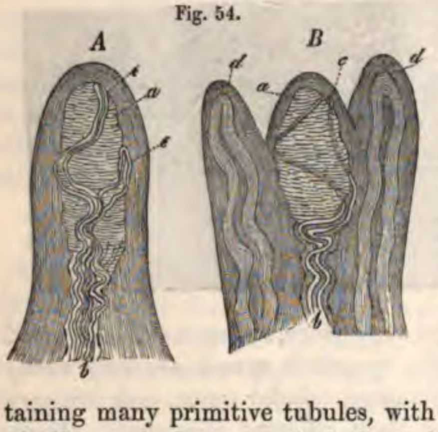


Fig. 54. Two *papillæ* from the extremities of the fingers, without epithelium and with axile corpuscles, *a*, and nerves, *b*. *A*. Simple *papilla*, with four nerve-fibres and two terminal loops, *c*. *B*. Compound *papilla*, with two vascular points with capillary loops, *d*; and one nervous point with a terminal loop, *e*.

(whether in all the fibres is as yet undecided) in man and in animals actual divisions of the *primitive tubules,* so that they divide, generally at an acute angle, into two; and from the plexus itself, the tubules finally enter the base of the *papillæ* in pairs, in order to run to their extremities, and there unite in a loop.

The elements of the nerves of the skin, exhibit no striking peculiarities; the diameter of some, in the trunks in the subcutaneous cellular tissue, is still as much as 0·005—0·006‴, and also in the deepest part of the *corium,* whilst they become finer and finer outwards. In the terminal plexus I find they vary according to the locality, from 0·003 to 0·0016‴, in the *papillæ* from 0·0008—0·002‴. In the hand and foot the finest tubules vary between 0·0012—0·002‴; in the *glans penis,* in the lips and nose, on the other hand, only from 0·0008—0·0012‴.

[R. Wagner has recently published some statements ('Allg. Zeitung,' Jan., Feb., 1852; 'Götting. Nachricht,' Feb. 1852), according to which the relations of the nerves of the skin have hitherto been entirely misconceived. From the investigations of G. Meissner and himself, which were instituted upon the nerves of the palm of the hand, Wagner divides the *papillæ* into nervous and vascular. The former are said to contain a peculiar oval corpuscle in their axis, which consists of superimposed saccular or band-like laminæ, resembling a fir-cone, and this structure is regarded by Wagner as a peculiar sensory apparatus, and named by him "tactile corpuscle" (*corpusculum tactûs*). Into these the nerves—1 to 3 fine dark-bordered tubules—are said to enter from below, or from the side, and to terminate within them, either free, or perhaps divided into many delicate branches. Wagner found these corpuscles to be most abundant in the points of the fingers, and that they were more and more rare towards the wrist. I have considered it requisite to investigate these assertions, which are made with much confidence, particularly as Wagner grounds upon them great expectations for the physiology of the sense of touch, and the following are the results at which I have arrived.

Independently of the vessels and nerves, the papillæ consist,

in the main, of a sometimes more homogeneous, sometimes more distinctly fibrillated collagenous substance, which there is no reason to distinguish from connective tissue, and of fine elastic fibres in different stages of development, as fusiform cells (corpuscles of the connective tissue, of Virchow), cell networks, isolated fine elastic fibres and fibrous networks. These elements are so distributed, that in most *papillæ* a *cortical* layer and an *axile* tract can be distinguished. In the former the fibrous elements are disposed longitudinally, and the connective tissue is often distinctly fibrillated, with the exception of the most superficial layer, which forms a clear, homogeneous but not separable margin. In the latter, on the other hand, the substance is more uniform and clear, and in many places is separated from the outer layer by transverse elastic fibres. When these latter, true elastic fibres are not very closely disposed, no one would be led to consider that there is anything peculiar in this arrangement; but undeveloped and very close together, as they are in Wagner's corpuscles, it is otherwise. These are, in fact, nothing but the clear axis marked by transverse nuclei and nucleated fibres, which I have already described; and, if no reagents be added, they present no other appearance than that which I have figured in my 'Microscopic Anatomy,' fig. 4, or in fig. 48 of this work.

Dilute solution of soda, of which almost solely, I have availed myself in investigating the course of the nerves in the papillæ, often does not render their contour at all more distinct, and I therefore paid no further attention to their structure; while, on the other hand, acetic acid, which was also employed by Wagner and Meissner, brings out the axes of the papillæ generally, though not always, as oval, or cylindrical, more sharply-defined bodies, to which the numerous transverse striæ give a certain vague similarity to a fir-cone (fig. 54). In its more intimate structure, such an "axile corpuscle," as I call it, does not consist of superimposed discs, as Wagner supposes, but of an internal mass of homogeneous connective tissue, which is most distinct in transverse sections, and when viewed from above; and of an external generally single layer of undeveloped elastic tissue, which, in the form of fusiform cells, probably connected together and, more or less, drawn out into fine fibres, with shorter or longer nuclei

(these last were also seen by Wagner), closely surrounds the internal substance in which here and there similar corpuscles also appear to be contained. *Morphologically*, then, such a corpuscle is by no means peculiarly constructed, but resembles the axis of certain other papillæ (*e. g.* of the sole of the foot), which are surrounded by true elastic fibres, particularly their often less-developed summits; it is very similar, again, to the bundles of connective tissue, with elastic fibres wound around them, such as are found in the *corium*; indeed, the difference consists principally in this, that the axis-corpuscle contains more undeveloped elastic tissue; a circumstance easily comprehensible, since the *papillæ*, as compared with the cutis itself, consist altogether of a tissue which is in a more embryonic state.

With regard to their occurrence, axile corpuscles of the kind here described occur only in certain papillæ; and, in fact, so far as my investigations hitherto extend, only in those of the *palm and surface of the hand, the red edges of the lips*, and *the tip of the tongue*, not in those of the toes, thorax, back, *glans penis, nymphæ*, and only rarely in those of the back of the hand and of the sole of the foot. In the hand they appear especially in the *compound papillæ*, in particular cusps one or two together, which may project more or less, and are sometimes shorter, frequently longer; they occur more rarely in the simple *papillæ*, as oval or cylindrical bodies, occupying $\frac{1}{3}$ to $\frac{2}{3}$ the width of the summits of the papillæ, and $\frac{1}{4}$ to $\frac{1}{2}$, or as much as $\frac{3}{4}$ the length. In the points of the fingers they occur in the proportion of 1 to every 2—4 *papillæ*; in the first phalanx, on the other hand, in the length of $1'''$, only 2—6 are to be found, and in the palm they are still more rare. Frequently the axile corpuscles exhibit local constrictions, especially after the addition of acetic acid, or are even spirally contorted, so that they often have a certain similarity to a bundle of connective tissue treated in the same way, or with a spiral sudoriparous duct. Upon the back of the fingers and in the heel there appeared, in many individuals, to be no axile corpuscles in the papillæ; in a small number, however, they were to be found even here, but scattered and small, in a few papillæ. In the lips, I saw in two individuals axile corpuscles similar to those in the hand, in one they were wanting. They existed only in that part of the red margin of the lip, which is visible when the mouth is closed; they were very minute, and

were placed partly in small projecting points of the larger papillæ, partly in depressions between two of their processes. In the *tongue*, in which, according to Wagner, something similar to his corpuscles appears to exist, I met, in two cases with no axile corpuscles; whilst, in a third, I found them tolerably well developed in the *papillæ fungiformes* of the point of the tongue (whether they are to be found in the posterior ones I know not), whilst they were wanting in the *p. filiformes* and *p. circumvallatæ*. In the *p. fungiformes*, one or many were situated in the point of the principal papilla, without extending into its simple processes, and therefore lay, as it were, at the bottom of a terminal pit, surrounded by the simple papillæ.

With regard to the *course of the nerves* of the skin, Wagner confirms the fact discovered by me, that even in man the primitive tubules divide in the terminal plexuses (which I have recently also observed in the hand, the lips, and the tongue); and he further states that, in the palm at least, only those papillæ contain nerves which possess the axile corpuscles, while they have no vessels. As regards the latter important circumstance, all those who have occupied themselves more particularly with the investigation of the skin, must be aware that nerves are not to be found in all the papillæ; but seeing the difficulty of discovering the nerves in a dense organ like the skin, no one has thought it requisite on this account to depart from the old notion that every papilla contains a nerve, and is therefore a tactile process. Wagner, having observed the sharply-defined axile corpuscles of the hand, appears to have been surprised that they occurred only in certain papillæ, and that these had nerves; and struck with this circumstance, adopted the view referred to. As for myself, having again made long-continued investigations into the skin of the palm of the hand, I find that those points of the papillæ, or those independent papillæ, which contain axile corpuscles, do generally exhibit dark-bordered nerve tubules very distinctly; but from this I should, for the present at any rate, by no means be led to conclude that the other papillæ contain no nerves, but only vessels.

If it be considered that dark-bordered nerve-tubules, though indeed rarely in proportion, are contained in vascular papillæ

without axile corpuscles, in the hand; furthermore, that in other places, as in the sole of the foot and the lips, such papillæ are found; and finally, that the investigation of the cutaneous nerves is very difficult, it seems more judicious to suspend one's judgment upon this question, especially as it is possible, that pale, non-medullated nerve-tubules, similar to those which I discovered in the skin of the Mouse, exist in man also. However, I am by no means disinclined to agree with Wagner thus far, that in the palm it is almost exclusively the papillæ with axile corpuscles which contain dark-bordered nerves, for to say the least, it is very remarkable that in these papillæ the nerves are so readily and satisfactorily displayed. As to the possible existence of non-medullated fibres in the papillæ without axile corpuscles, it is certainly too soon to express any definite opinion. With regard to the vessels, it is incorrect, unconditionally to deny their existence in those papillæ which contain nerves. In the compound papillæ it is unquestionably true, that the cusps with axile corpuscles and nerves frequently contain no vessels; at other times, however, even these contain a capillary loop, and this is still more frequently the case in the simple papillæ with nerves. In the *lip*, the papillæ containing nerves, whether they possess axile corpuscles or not, contain vessels for the most part, if not always, and there are relatively very few papillæ in which no nerves are visible. The tongue possesses vessels and nerves in all the larger papillæ; on the other hand, I have as yet been unable to discover nerves in the simple papillæ buried in the epithelium. It is yet to be ascertained how the nerves are disposed in other parts of the skin. It is surprising to me, that even in the sole of the foot, dark-bordered nerve-tubules can so rarely be perceived in the papillæ, while in many situations they cannot be found at all.

Further investigations are required to determine to what extent dark-bordered nerves are distributed in the papillæ of the skin; whether, perhaps, non-medullated fibres occur instead of them; or whether, in certain situations, the nerves do not enter the papillæ at all, but end in the well-known superficial plexus at their base.

With respect to the dark-bordered nerves in the papillæ of the hand, Wagner is wrong in asserting that the nervous

loops which I have figured are blood-vessels. He has only imperfectly seen the nerves of the papillæ in question, perhaps on account of his having preferred the use of caustic soda, which more easily destroys them. Latterly, in making very delicate investigations, I have used only acetic acid, and have arrived at the following results:—Each point of a papilla, or each papilla with an axile corpuscle, generally contains two, or as frequently happens at the points of the fingers four, dark-bordered tubules, which, surrounded by a *neurilemma* which has escaped previous observers, pass upwards through the axis of the papilla to reach the base of the axile corpuscle, as a fine, convoluted nervous twig of 0·006—·012‴ in thickness. Here the nerve frequently becomes invisible, so that, as has happened to Wagner, one may be led to believe that it enters the corpuscle, which is seated upon it, as upon a stalk, and there ends. However, if a number of fresh preparations be treated with acetic acid and examined, the conviction is soon arrived at that this is merely apparent, the nervous tubules in reality proceeding *along the outer surface* of the corpuscle, either as far as its point, or very nearly so. In the meanwhile they either remain together or take an isolated course. In both cases their neurilemma becomes excessively delicate, appearing finally to vanish entirely, while the nerves themselves surround the axile corpuscle, passing round it either more directly, though in a slightly undulating course, or forming one or several spiral-coils (fig. 54, *B*). As regards the actual termination of the nervous tubules, I retain the opinion I formerly expressed, inasmuch as, in at least six cases, I have again most distinctly seen *loops* (fig. 54). It is, however, always difficult to observe them, and very frequently impossible, in spite of every exertion; and therefore, as we are all liable to error, I will blame no one for considering the termination of the nerves of the papillæ to be unknown, or for believing in the existence of free ends, which perhaps also exist, and, at any rate, very frequently *appear* to exist. I only state what, according to my best belief, I have seen; and while I have no prejudice in favour of loops, neither can I see anything alarming in their existence. This much, however, is certain, that Wagner has not traced the nerves in the papillæ so far as they may be traced, and therefore, at present at all events, can lay no claim to

a decisive voice in the matter. How the nerves in the papillæ of the lips, tongue, and elsewhere, are disposed, I have not yet ascertained with certainty; but with regard to the first of these, I believe I can also affirm, that they do not terminate *in* the axile corpuscles, but either merely pass by them or wind round them. In the lips, in a single instance, I found well-marked *nerve-coils* in small papillæ, or at the base of the large ones.[1]]

§ 38.

Development of the Cutis.—The following may be taken as a general sketch of the development in the fœtus, of the *cutis*, in the broadest sense of the term. It consists at first of cells, which though not in man, yet in animals (the Frog, for instance) may be easily traced back to the earliest formative cells of the embryo. A considerable proportion of these cells are changed into connective tissue, becoming fusiform, coalescing, and eventually being converted into bundles of fibrils; a process which appears to occur first in the *fascia superficialis*, the subcutaneous connective tissue, then in the *pars reticularis* of the *corium*, and finally in the papillary layer. Another portion of the cells are converted into vessels and nerves, as can be seen even in man, and very beautifully in the Batrachia (see my Memoir in the 'Annales des Sciences Naturelles,' 1846); while a third, growing and developing fat in its interior, becomes elastic fibres and fat-cells (vide supra, § 23). The first foundations of all these parts having been laid, they continue to increase in a manner which is not yet exactly made out. The cutis obviously grows from within outwards (so that the papillæ arise and are developed last of all), partly by the growth of its primitive elements, partly at the expense of cells, which are perhaps mostly of new formation, and do not proceed from the original formative cells. The *panniculus adiposus* also increases, partly by the increase of the cells, of which it at first consists, partly by the subsequent development of others, as well as of connective tissue and vessels. In this manner the skin grows for a long time after birth. In children

[1] [Mr. Dalzell, in a communication read before the Edinburgh Physiological Society, January, 1853 ('Monthly Journal of Medical Science,' March, 1853), confirms Kölliker's account of the *corpuscula tactûs* in all essential points.—Eds.]

below 7 years of age, for example, the cutis is, according to Krause, only half as thick as in the adult, until at last, though at a time which is as yet undetermined, the new development of cells ceases, as at a later period, perhaps, does the extension of those elements, cells, fibres, &c., which are already formed. The fat-cells of adults, in which the process of growth is especially obvious, according to Harting, are in the orbit twice, in the palm three times as large as in the new-born infant; whence it results, that they increase in size in proportion to the parts of the body to which they belong.

[In embryos of two months the skin is 0·006—0·01‴ thick, and wholly composed of cells. At the third month it is about 0·06‴, and already presents tolerably distinct connective tissue. In the fourth month the first lobules of fat appear, and the ridges of the hand and sole of the foot. From the seventh month onwards the *panniculus adiposus* is rapidly developed, and at birth it is relatively thicker than in the adult.]

§ 39.

Physiological Remarks.—If we attempt to harmonise the anatomical data here brought together, with the phenomena of sensation exhibited by the skin, we meet with considerable difficulties. The more intimate anatomy of the skin, as it is here detailed, fails to demonstrate nerves in all the papillæ, or even in the majority of them; and yet experiment teaches that though all points of the skin may not feel with the same delicacy, they are all nevertheless sensitive. I hoped to be able to submit Wagner's doctrine of the absence of nerves in many papillæ to experimental proof, by examining the sensitiveness of various parts of the body with the finest possible English sewing needle. At first I really thought that I had found some places which were quite insensible, whilst in others the slightest touch produced sensation; but on carrying the investigation further, it appeared that the very same place was often sometimes sensible, sometimes not; so that, finally, I came to the conclusion that the very smallest portions of the skin are sensitive. But since even in the palm of the hand the papillæ containing nerves are widely dispersed, and in other places occur but rarely or even not at all, it only remains

either to assume the existence of non-medullated nerve-fibres in all the papillæ, or to have recourse to the nervous plexus at the base of the papillæ. I should unhesitatingly prefer the latter explanation, were it not: (1) that these plexuses are in many places so very scanty, and (2) that the slightest touch of the epidermis produces sensation; for the present, therefore, I believe this must remain an open question.

If we are not in a condition to understand how it is that every point of the skin is sensitive, still less are we competent to explain the different kinds of sensations. In this respect the following very general statement may be made.

The excitement of the terminations of the nerves in the outermost parts of the cutis and the papillæ is either direct or indirect. The former as it is produced, for example, when the cutis is laid bare, by penetrating instruments and by fluids, is much more intense than that which takes place through the mediation of the epidermis, one of the functions of the latter being to act as a defence against too violent impressions, and to blunt them according to its greater or less thickness. It can now be partly explained on anatomical grounds, why the delicacy and vivacity of the sense of touch are not everywhere equal, why they are less upon the hairy scalp, the back, the two upper divisions of the extremities, than on the face, on the *genitalia*, the hand and foot, the chest and abdomen. In the first place, where the tactile sense is delicate, the epidermis is in itself thin, as upon the eyelids and face, or has, at least, a thin horny layer, as upon the *penis* and *clitoris*, whilst upon the back and extremities it is considerably thicker. Yet this circumstance is not a sufficient explanation, for parts with a thicker epidermis, as the palm of the hand and the sole of the foot are delicately sensitive, more so, in fact, than others with a thinner covering, as the back of the hand and foot. Another condition must here obviously come into play, and it is, I think, that the skin is not *equally well provided with nerves in all its parts.* Simple inspection teaches that the nerves upon the palm of the hand and the sole of the foot are more numerous than upon the back of the hand and foot; upon the *glans penis* and *clitoridis*, the nipple, the face, they are more abundant than upon the abdomen, back, and thigh, &c. &c.; and this is to some extent confirmed by my

measurements of the sensitive roots of the spinal nerves (*vide* 'Mic. Anat.,' p. 433). With the number of the nerves, is connected that of the actually demonstrable dark-contoured nerves in the papillæ and the superficial nervous plexus, for nowhere is this more considerable than in the points of the fingers, the lips, the tip of the tongue, and the glans penis.

As to the *local sensibility* of the skin, it is the province of anatomy, especially, to afford information, with regard to these two points: 1, how it is that we do not distinguish with the same clearness and exactness, in all parts of the body, the point at which a single irritation is applied: and, 2, why two stimuli operating at the same time, under certain circumstances, appear double, under others single (Weber's experiment). I think that Weber's experiment cannot be explained by the mode of distribution of the peripheral nerves, but depends very probably upon their central relations. It seems to me to be simplest to assume, that every peripheral end of a nerve is capable, when irritated, of producing a conscious sensation, but that, on account of the small number of nervous fibres (in the *cerebrum*) which unite these with the seat of consciousness, if many contiguous, or even more distant, cutaneous nerves are excited, only a single conscious sensation results. In this case, the nerves of acutely sensitive parts must be connected with the seat of consciousness by more numerous intermediate fibres than those of other localities, and at the ends of these fibres, also, we must suppose a sort of interlacement to take place. Upon this hypothesis, the former of the two points might be explained. A local irritation is, indeed, felt locally; but, according as the nerves implicated are united with the brain by more or fewer conductors in the spinal cord, are we able to assign, more or less exactly, the precise spot; so that, in some cases, the limits of error will not exceed $\frac{1}{2}'''$—$1'''$, while, in others, they may extend to $1''$—$1\frac{1}{2}''$ and more.

E. H. Weber has endeavoured to demonstrate, in his last able Treatise upon the sense of touch, that it is only the termination of the nerves in the skin, not the fibres in the nervous trunks, which are the mediators of the sensations of pressure, warmth, and cold; and he has expressed a supposition, that tactile organs as yet unknown may exist in the

skin. R. Wagner believes that he has, in fact, found these organs in his so-called *corpuscula tactûs,* and he supposes that, composed as they are, according to him, of superimposed membranes, in the interspaces of which a very minute quantity of fluid is lodged, like elastic cushions, or a bladder filled with water, they are specially fitted to receive impressions from the epidermis at the extremity which is directed towards it, and to transmit them to the ends of the nerves which lie in and upon them.

In my opinion, Weber's view of the greater sensibility of the terminations of the nerves in the skin, can hardly be doubted; but, on the other hand, there is no obvious reason, *à priori,* why peculiar hitherto unknown organs should exist to that end; nor why the condition to which I have already referred, the more *isolated course* of the fibres of the nervous tubules in the papillæ and terminal plexuses, their fineness, *superficial position,* and the *delicacy* or *absence* of the *neurilemma,* may not abundantly suffice as an explanation. That Wagner's so-called *corpuscula tactûs,* my axile corpuscles, are not tactile organs in the sense intended by Weber, is easily demonstrable. Independently of the erroneousness of his views of their structure, and of the fact that the nerves are not distributed in them, but only proceed along them, outside, in order, in many cases, to terminate even beyond them—we find *that all the essential functions of the skin are also performed without such corpuscles.* The feeling of warmth and cold, of orgasm, of tickling, of pressure, of pricking, of burning, of pain, are found partly over the whole surface of skin, partly in places where these corpuscles are certainly absent, which sufficiently shows *that they have not in the remotest degree the signification ascribed to them by Wagner.* However, it is not likely that they exist for nothing in those particular localities, in which the sensibility to pressure is the greatest, and which we use especially as tactile organs, as the ends of the fingers, the point of the tongue, and the border of the lips; and I consider them as parts, *which, in consequence of their being composed principally of dense, imperfectly-formed elastic tissue, confer a certain solidity upon the points of the papillæ, and serve as a firm support for the nerves,* in consequence of which, a pressure, which in other situations is not sufficient to

affect the nerve, here takes effect. They would, in fact, be organs, like the nails and phalangeal bones, not essential and indispensable to the sense of touch, but only conferring upon it a greater acuteness than elsewhere. If, in this sense, they are to be called *tactile corpuscles,* I have nothing to say against the term, but then the phalanges and the nails, the "whiskers" of animals, &c., equally deserve the name of tactile organs.[1]

The contractility of the skin is exhibited in the wrinkling of the scrotum and of the skin of the *penis,* the erection of the nipple, and the occurrence of the so-called *cutis anserina.* It depends upon the smooth muscles of the skin already described, which, as Froriep and subsequently Brown-Sequard and I have found, contract by electricity, inasmuch as by this means, even in the living subject, the *cutis anserina,* the erection of the nipple, and, in recently-executed persons, a wrinkling of the *scrotum* can be produced. In the erection of the nipple by gentle mechanical irritation, the whole areola becomes diminished by the contraction of its circular fibres, and thus protrudes the nipple whose muscular fibres, in this case, seem to be relaxed. Cold causes the areola and the nipple to contract, both becoming small and firm. The *cutis anserina,* which consists in wholly local contractions of the portions of the skin around the hair sacs by which their apertures are protruded conically, is explained simply by the existence of the muscles which I discovered, and which pass obliquely from the superficial part of the cutis down to the hair sacs, and when they act, extrude the sacs, and retract those portions of the skin whence they arise. The assumption of a contractile connective tissue in the skin, as well as in other parts, I must repudiate here, as I have already done (Mittheil. der Züricher Gesellschaft, 1847, p. 27), because the smooth muscles, which can be microscopically demonstrated in the skin, and whose contraction by galvanism may be experimentally shown, sufficiently account for all the contractile phenomena which it exhibits.

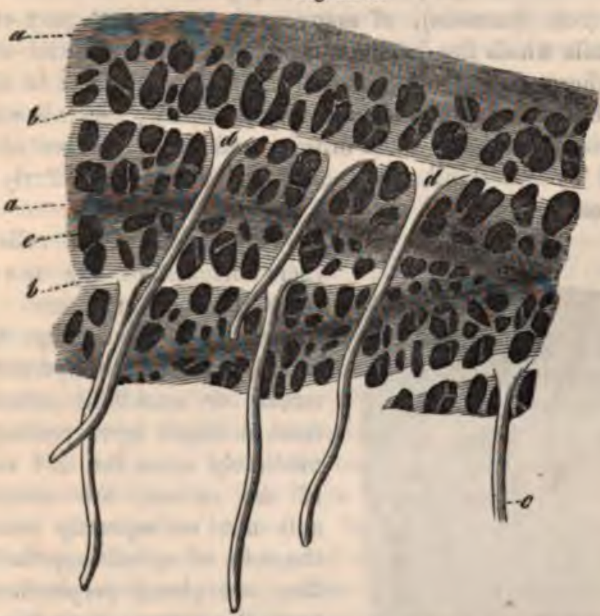
[1] [See, however, Wagner's reply to Kölliker, 'Ueber die Tastkörperchen,' in Müller's 'Archiv,' August, 1852.—Eds.]

B. EPIDERMIS.

§ 40.

The *corium* is everywhere covered by a semitransparent membrane formed wholly of cells, and containing neither vessels nor nerves,—the *epidermis,* which applies itself exactly to all the elevations and depressions, and which accordingly upon

Fig. 55 *A.*



its inner surface presents an exact cast of the outer surface of the *corium,* the convexities and concavities of course being reversed. Upon its outer surface, also, the epidermis, to some extent, represents the form of the *corium,* since the more marked elevations and depressions, such as the ridges of the palm of the hand and of the sole of the foot, the folds at the joints, muscular insertions, &c. are expressed in it,—the latter even

Fig. 55 *A.* Surface of the palm, from within: *a,* ridge answering to the groove between the ridges of the cutis; *b,* a similar one corresponding with the cleft between the rows of papillæ; *c,* sweat ducts; *d,* broader points of insertion of these into the epidermis; *e,* depressions for the simple and compound papillæ.

more strongly; on the other hand, the papillæ produce either no perceptible projection, or hardly any.

The *epidermis* consists of two layers, chemically and morphologically distinct, and which are separated by a tolerably sharp line of demarcation, viz., the *mucous layer* and the *horny layer*.

§ 41.

The *mucous layer, stratum Malpighii, rete* or *mucus Malpighii* (*rete mucosum*), of many authors, is that part of the epidermis which lies immediately upon the *corium*, and almost everywhere appears undulated; in many places it is distinguishable even to the naked eye by its colour, which is whitish or variously tinged with brown, and it is further characterized by its small, soft, easily destroyed, peculiarly disposed cells.

Fig. 55 *B.*

The form of these cells and their disposition are not the same in all localities. The innermost of them (fig. 55 *b*), which, without interspersed free nuclei or semi-fluid substance, form a single layer resting immediately upon the free surface of the *corium*, are elongated, and not unfrequently resemble the cells of cylinder-epithelium; they are placed perpendicularly upon the *corium;* their length is about from 0·0033—0·006‴, their breadth 0·0025—0·003‴. Upon these immediately follow, in most places, elongated or even round cells of 0·003—0·004‴ in many layers; but in a few localities, as in the hand and foot, at the free margin of the eyelids, in the mucous layer of the nails and hairs (*vide infra*), there are interposed here and

Fig. 55 *B.* Perpendicular section of the skin of the Negro (from the leg), × 250: *aa*, cutis-papillæ; *b*, deepest intensely-coloured layer of perpendicularly elongated cells of the *stratum mucosum; c*, upper layer of the *stratum mucosum: d*, horny layer.

there, between the rounded and elongated cells, one, two, or even three layers of similarly elongated and perpendicularly disposed elements, so that the mucous layer, on account of the numerous strata of perpendicular cells, has a striated appearance in its deepest part, under a low power. This character is the more striking, since the other elements of the mucous layer, the further they are followed from the first, round cells outwards, become thinner in another direction, *i. e.*, become horizontally flattened (fig. 55 *c*), and finally in the uppermost layers are transformed into thick vesicles, 0·006—0·016‴ broad, and 0·002—0·008‴ thick. At the same time, from their mutual pressure, they acquire a polygonal form, which may even be recognised in isolated cells.

All the cells of the mucous layer agree, in essential points, in their structure, and are nucleated vesicles distended with fluid. Their membrane is pale, often difficult of demonstration in the smallest, frequently quite distinct, always delicate, thicker in the larger ones, yet by no means to be compared to that of the cells in the horny layer. The contents are never quite fluid; but also, excepting in the coloured epidermis (*vide infra*), never normally contain larger particles, granules or fat-drops for example; but are finely granulated, with more or less clearly-defined granules, which invariably diminish in number in the more external cells. The nucleus, lastly, is small in the smallest cells (0·0015—0·0025‴), in the large, of greater size (0·003—0·005‴); globular or lenticular, in the round and flattened cells; elongated, in the elongated cells. In the larger cells it appears obviously vesicular, often with a nucleolus, and lies centrally in the midst of the contents; in the smaller it is apparently more homogeneous, without any visible nucleolus, and so disposed that it is not unfrequently in contact with one part or other of the cell-walls.

§ 42.

The horny layer (*stratum corneum*), forms the external semi-transparent part of the epidermis, which in white people is colourless, and is composed almost wholly of uniform cells metamorphosed into plates. The deepest plates are still very similar to the uppermost cells of the *stratum mucosum;* but even in the second or third layer we find the widely different

epidermic or *horny plates.* They (fig. 56. 1, 2, 3) are, in fact, plates of moderate thickness, which in the lower and middle parts of the horny layer retain tolerably regular polygonal (4-5-6 sided) and smooth surfaces; in the upper layers, on the other hand, they present more irregular outlines, are variously crooked and curved, and thence often appear to be wrinkled and folded. These plates must be regarded as cells, completely flattened, and containing a very minute quantity of viscid fluid; and not, as might at first be imagined, as homogeneous lamellæ, composed throughout of the same substance; for by the addition of various reagents, especially of acetic acid and of potass, they swell up and assume the form of vesicles (fig. 57); at the same time, a rudimentary nucleus becomes obvious in a few, particularly in those from the middle and inner layers, but by no means in the majority of them, in the form of a flat, homogeneous, rounded or elongated corpuscle, 0·003—0·004‴ in length, and 0·002—0·003‴ in breadth, which, especially when seen from the side, is easily recognised by the dark contours which it then presents. The size of the plates of the ordinary horny layer varies from 0·008—0·016‴, and in the outer layer it is commonly somewhat greater than in the inner. Upon the body of the *penis* the cells measure 0·008‴—0·012‴; upon the *glans*, the largest are 0·016—0·02‴; upon the outer side of the *labia minora* 0·012—0·02‴; on the *labia majora* 0·01—0·016‴. These last, larger

Fig. 56.

Fig. 56. Horny plates of man, × 350: 1, without addition, viewed from the surface one with a nucleus; 2, from the side; 3, treated with water, granular and dark; 4, nucleated plate, such as occur on the outer surface of the *labia minora* and on the *glans penis*.

cells, all possess distinct nuclei, and are almost identical with the epithelial plates, *e. g.*, of the cavity of the mouth and of the *vagina* (fig. 56. 4.)

Whilst the *stratum Malpighii*, except in its upper layer, is but indistinctly laminated, a clear lamination is obvious in the horny layer, inasmuch as its plates applied together horizontally, form strata in number proportionate to the thickness of the horny layer (fig. 55). It must not be imagined that these strata are distinctly defined from one another; they are connected by their surfaces, and can only be detached and demonstrated adhering together in numbers, by dissection, which is much facilitated by boiling or macerating the epidermis. The innermost, like the *stratum Malpighii*, taken altogether, exhibit a wavy course wherever papillæ exist, projecting outwards over the points of the papillæ and following the depressions between them. This takes place in the most striking manner where very much developed papillæ coexist with a moderately thick *rete Malpighii*, especially in the palm and in the sole of the foot, in which (see the figure in the section on the sudoriparous glands) the horny layer penetrates so deeply between the papillæ, that its deepest cells are on a level with half their height: where the papillæ are smaller, the horny layer sinks less deeply between them, or even lies quite flat upon the *stratum Malpighii*, as is the case where the papillæ are absent. From this cause the boundary line between the horny layer and the *stratum mucosum* in perpendicular sections, is sometimes straight, sometimes wavy, with smaller or greater elevations and depressions. The other parts of the horny layer take a more even course the further they are from the mucous layer; yet not merely in the hand and foot, where, as is well known, the ridges of the *corium* are marked externally upon the epidermis, but in many other localities a slightly wavy course of the uppermost layers may be perceived in perpendicular sections, and slight elevations indicate externally the points beneath which the papillæ are seated. In the separate lamellæ the plates are sometimes irregular, sometimes arranged circularly, as around the excretory ducts of the glands and hair-follicles, and also round the papillæ on the palm of the hand and sole of the foot, as may be seen most readily at the apertures of the sudoriparous glands.

§ 43.

As regards the colour of the epidermis, in the white races, as has been said, the horny layer is colourless and transparent, or slightly yellowish, the mucous layer yellowish white, or brownish. The colour is deepest in the *areola* and in the nipple, passing even into blackish-brown, especially in women during pregnancy and after they have borne children: it is less intense in the *labia majora*, the *scrotum*, and the *penis*, where for the rest it varies greatly, being sometimes almost entirely absent, sometimes very distinct, and is least considerable in the axilla and round the anus. Besides these situations, which in most individuals are more or less tinged, in the dark-complexioned more than in the fair, a lighter or more deeply coloured, frequently very dark pigment is deposited in various other localities in the *stratum Malpighii;* in pregnant women in the *linea alba*, and in the face (rhubarb-coloured spots); in persons who are exposed to the sun, in the face, especially the brow, chin, and cheeks; in the neck, the thorax, the back of the hands, the forearm; and in dark persons over almost the whole body. These tints are not produced by special pigment-cells, but are seated in the common cells of the mucous layer, round whose nuclei a finely granular or more homogeneous colouring matter or actual pigment granules are deposited. When the skin is only slightly coloured, it is mostly only the neighbourhood of the nuclei and in fact, only of the lowermost layers of cells which is implicated, so that in perpendicular sections the papillæ are seen to be surrounded by a yellowish fringe; darker shades are produced by the extension of the colour to two, three, four, and more layers of cells, and over the whole cell contents; sometimes by a darker coloration of the deepest layer of cells; the two conditions commonly coexisting. The horny layer also of the coloured places of the skin, has according to Krause, its cell-walls slightly tinged; this appears, however, only upon comparing them with those of uncoloured parts of the skin, and only in the more deeply-tinged parts. In the Negro, and the other *coloured human races*, it is also only the epidermis which is coloured, whilst the *corium* completely resembles that of Europeans. The pigment, however, is far darker and more abundant. In the Negro (fig. 55), in whom, as regards the

arrangement and size of the cells, the epidermis is precisely like that of the European, it is the perpendicular cells of the deepest part of the mucous layer which are darkest (dark brown or blackish-brown), and they form a sharply-marked fringe contrasted against the clear *corium*. To these succeed clearer but still brown cells, which are accumulated particularly in the depressions between the papillæ, but are also found on their points and lateral portions in many layers; finally at the boundary close to the horny layer there follow brownish-yellow or yellow, often rather pale, more transparent layers. All these cells are coloured throughout, with the exception of their membranes, and especially the parts round the nuclei, which, in the internal layers, are by far the darkest portions of the cells. The horny layer of the negro also inclines to yellow or brownish. In the yellowish skin of a Malay head in the anatomical collection at Würzburg, I find the same appearance as in a dark-coloured European *scrotum*. It follows, then, that the epidermis of the coloured races is, in no essential point, distinguishable from the coloured regions in the white man, and it even agrees in nearly all respects with that of certain localities (the areola of the nipple, for instance).

[*Pathological* coloration of the epidermis (freckles, mothers' marks, &c.) according to Simon, Krause, Bärensprung, and my own observations, is produced exactly as the more intensely-coloured spots in the white man, and as the colour of the negro's skin. Pigment deposits in the *corium* and in the papillæ, such as may be seen in cicatrices, after chronic inflammation of the skin, and frequently as in *ichthyosis* and many *nævi*, associated with a coloured epidermis, in which the pigment is developed directly from the blood-corpuscles and their colouring matter, must be carefully distinguished from the foregoing. Numerous instances of partially or entirely white Negroes and of black Europeans, not as a consequence of change of climate, but as a congenital or subsequently arising abnormal condition of the skin, have been noticed (see Hildebrandt.—Weber, II, fig. 526; Flourens, Compt. rendus XVII). But, for the future, it will have to be remembered, so far as the dark coloration of Europeans is concerned, that it may also arise from a deposition of the colouring matter of the bile.]

§ 44.

The thickness of the epidermis as a whole, varies exceedingly, depending especially upon that of the horny layer. It measures:

$\frac{1}{75}$ — $\frac{1}{50}'''$ upon the chin, the cheeks, and brow, in the external auditory passages, and upon the eyelids:

$\frac{1}{50}$ — $\frac{1}{25}'''$ upon the bridge of the nose, on the breast and nipple in the female, on the back of the toes and fingers, upon the neck and back, on the inner and outer side of the thigh, on the *scrotum* and the *labia minora:*

$\frac{1}{25}$ — $\frac{1}{16}'''$ on the edge of the eyelids, on the male chest and nipple, the hairy scalp, the chin, *penis*, prepuce, and *glans penis:*

$\frac{1}{16}$ — $\frac{1}{10}'''$ on the red external parts of the lips, on the back of the hand:

$\frac{1}{10}$ — $\frac{1}{7}'''$ on the flexor side of the fingers and toes:

$\frac{1}{5}$ — $\frac{1}{2}'''$ on the palm: and—

$\frac{3}{4}$ — $1\frac{1}{3}'''$ on the sole of the foot, in which two latter localities the variations are greatest, independently of the circumstance, that in the furrows and at the joints the skin is thinner than elsewhere.

With regard to the proportionate thickness of the horny and mucous layers I find, in some localities, that the latter is constantly thicker than the former; *i. e.*, in all parts of the face, in the hairy scalp, in the *penis*, the *glans*, the *scrotum*, the nipple, and the skin of the thorax in man; in the *labia majora* and *minora*, on the back and neck. Here the mucous layer is 3—6 times, or 2—3 times as thick as the horny layer, according as its thickness is measured from the bases or from the points of the *papillæ;* in a few of the localities mentioned, however, the *stratum Malpighii* is, in its thinnest parts, of the same thickness as the epidermis, as in the *glans*. In the rest of the body, both layers are either equal in thickness, as in the external auditory passage, and here and there upon the flexor side of the first two sections of the extremities, or the horny layer is 2 to 5 times thicker than the mucous, and in the thickest places even 10 to 12 times as thick.

The absolute thickness of the *stratum Malpighii* varies (at the base of the *papillæ*) between 0·007 and 0·16‴; where it is thicker than the horny layer, it measures in the mean 0·04‴; where it is thinner, 0·01—0·02‴. The horny layer by itself measures in many places only 0·005‴, in others 1‴ or more; when its thickness exceeds that of the *stratum Malpighii*, it is generally about 0·1—0·4‴, when it is less, 0·01‴.

§ 45.

Physical and vital Properties.—The epidermis is but little elastic, flexible in the living condition and not easily frangible, softer in the deeper than in the superficial layers. The cells contain, neither in their membranes nor between them, any demonstrable pores (apart from the sudoriparous ducts and hair-sacs, which, in a manner, have their outermost portion hollowed out in the epidermis), and form a very solid, hardly permeable substance. Many experiments, especially those of Krause, show, that the horny layer of the epidermis permits no fluids, except those which act chemically upon it, as the mineral acids and the caustic alkalies, to pass through it, either by pores, or by imbibition, or by endosmose and exosmose, while it readily takes up gaseous matters, or easily vaporizable substances (alcohol, ether, acetic acid, ammonia, solutions of chloride of iron in ether, of acetate of lead in alcohol), and gives them off (cutaneous evaporation). This conclusion is not invalidated by the undeniable passage of water, liquid substances, ointments, and even solid matters (sulphur, cinnabar), through the uninjured epidermis, since in these cases a mechanical intrusion of the substances, in and through the sudoriparous ducts and hair-sacs, or their penetration into the sweat-ducts, and mingling with the sweat, explains their absorption. The mucous layer, at any rate, is easily penetrated by liquids, as is sufficiently shown by pathological anatomy (exudations which penetrate the mucous and raise up the horny layer into a vesicle, the ready occurrence of absorption after the separation of the horny and the superficial portion of the mucous layer, by the action of vesicants.)

In their *chemical relations*, it is indeed well known how the cells and plates of the epidermis behave with regard to certain reagents, but there exists, at present, no perfectly satisfactory

total analysis of the epidermis, with regard to its two layers which differ so widely; and the organic combinations, also, which occur in it, are not sufficiently known.

The so-called *horn*, which forms the membranes of the horny-plates, is insoluble in water, easily soluble in concentrated alkalies and concentrated sulphuric acid, whence the skin, if wetted with these substances, feels slippery and greasy; there remains, however, a small residue insoluble in alkalies; concentrated acetic acid, also, dissolves it, first rendering it gelatinous, by which it is distinguished from the protein compound of the hair. It contains less sulphur than the hair and nails, which is perhaps the reason why salts of lead, mercury, and bismuth, colour the hair but not the epidermis. Besides these, Mulder finds in the horny layer a gelatinous matter, which is obtained by long boiling in water, and which would appear to be of a collagenous nature. The epidermis does not putrefy—it melts in the fire without bending or swelling up, and burns with a clear flame.

[The behaviour of the epidermis towards reagents is particularly of importance for the microscopist, on whose behoof I add the following account.

After long maceration in water, the epidermis becomes detached in portions, and under moderate pressure is resolved into a white powder, consisting of the isolated horny plates, and the uppermost cells of the *rete Malpighii*. Boiled in water, pieces of the horny layer break up into their elements much more readily. Boiled in concentrated acetic acid for 15 to 25 minutes, all the horny plates become perfectly isolated, forming a cloudy, whitish deposit in the test tube; they are exceedingly pale, so that they are often hardly visible under a full illumination; and are completely swollen up and changed into globular or elongated, distended, but always more or less flattened vesicles of 0·02—0·032‴ breadth, and 0·006—0·01‴ thickness, the nuclei when they are present being also pale and hardly to be perceived. The Malpighian layer becomes pale under the action of cold, concentrated acetic acid, the cells and nuclei being rendered more distinct. The cell-contents are partially dissolved: by longer action the contours of the deepest layers of cells become

invisible. The same thing occurs after boiling for four minutes.

Caustic potass and soda act differently, according as the solutions used are concentrated or diluted. In the latter case, immediately after the addition of the reagent, the horny layer is rendered more clear, it swells up and changes in a short time into a beautiful tissue of pellucid, globular vesicles, without nucleus or granules, and with sharp, moderately-thick contours, 0·02—·032''' in breadth, and 0·016—0·02''' in thickness. If concentrated, solutions of the caustic alkalies render the plates at first smaller, so that they measure only 0·012—0·016''', and are at the same time more wrinkled and pale, but with defined, dark contours; in the course of an hour they swell up so as to appear as cells, but it takes two or three hours to give them the aspect of the plates which have been heated with dilute solutions. Boiled with these fluids, even the dry horny layer swells up, in an instant, into the most beautiful tissue of cells, without either granules or nuclei (fig. 57), and at the same time the dissolving cell-contents, mixed with the alkali, are collected in the cells, into greater and smaller granular masses; after the action of the heat for five hours, all the cells disappear without leaving a trace, and yellowish and pale fat-drops in no great number, swim in the liquid. The cells of the Malpighian layer are still more acted upon by alkalies than those of the horny stratum: they swell up at once, and appear distinctly as delicate vesicles; these then dissolve, all but the uppermost two or three layers, which require a longer time, like those of the horny stratum, though less than the latter. The *nuclei* of all the cells withstand the operation of this reagent even less than the cells; whilst, when the latter are dissolved, a granular or striated substance remains behind, which is, probably, partly fat. *Concen-*

Fig. 57.

Fig. 57. Horny plates boiled with caustic potassa and distended; the contents partially and wholly distended, × 350.

trated sulphuric acid, in five minutes, causes the horny layer to swell up so much, that its elements, although still remaining flattened and irregular, appear quite distinctly to be vesicles; after half an hour they are somewhat more distended, and easily separable from one another. By boiling with this acid the plates swell up even in a minute, without exhibiting nuclei, and in two minutes they disappear without leaving any trace. Boiling in *dilute sulphuric acid* renders the horny layer hard and transparent, and dissolves it wholly in 4—5 hours. The cells of the *stratum Malpighii* are little altered by cold sulphuric acid: on boiling, their contours and nuclei at first become more distinct, but in about two minutes the whole is dissolved. *Nitric acid* colours the epidermis yellow, softens and changes it into xantho-proteic acid. The cells of the horny layers swell up somewhat, after a time, in the cold, and become granular; the *stratum Malpighii* is rendered granular and indistinct, and sharply defined from the horny layer. Upon boiling, the whole epidermis is entirely dissolved in half a minute. *Hydrochloric acid* does not tinge the epidermis, and in the cold renders the cells of the horny layer somewhat more distinct than nitric acid. After boiling for a minute the horny layer becomes a beautiful cellular tissue, exactly as after the addition of dilute solution of potass. In *carbonate of potass* the epidermis is hardly changed at all. After seventeen weeks it is hardened and easily cut with a knife. *Nitrate of silver* colours it violet or brownish-black, by the formation of oxide of silver, of chloride of silver, and of black sulphuret of silver, in consequence of the chloride of sodium and sulphur which it contains. Investigated microscopically with the help of *acetic acid,* the tissue of the epidermis is seen to remain quite unchanged, and minute dark granules are visible between its elements. *Nitrate of mercury* gives the epidermis a reddish-brown hue, sulphurets of the alkalies render it brown and black: many vegetable colours unite with it. In *alcohol* and *ether* it is insoluble, with the exception of the small quantity of fat which it contains.

From all this, it results, with regard to the elementary parts of the epidermis, that they are cells, which, however, as the alkalies show, do not everywhere present the same characters. In the *stratum mucosum* they are actual vesicles and easily

soluble—in the horny layer, scarcely so; and here, in fact, a distinction must be drawn between the resisting cell-membrane and the cell-contents, which swell up and disappear more readily; these, in the natural condition, form an apparently homogeneous simple plate, but the difference between them may be readily exhibited by reagents. In what parts the small quantity of collagenous substance, which has been noticed, has its seat, is not clear; perhaps it forms a portion of the contents, especially of the cells of the mucous layer, or belongs, it may be, to an intermediate substance between the cells, which, however, is not microscopically demonstrable. If the fat of the epidermis is not merely accidental, arising from the cutaneous secretions, it is most probably contained within the Malpighian cells.

Bruns, Todd and Bowman, Valentin and Bruch, recommend the use of alkalies for the investigation of the epidermic tissues, but their full importance was first shown by Donders (Mulder's 'Phys. Chemie,' p. 257, et seq., and 'Holländische Beiträge,' I u. II). They are now generally recognised as quite indispensable reagents for the investigation of the horny tissues; but, as Paulsen ('Obs. Microchem.,' &c. Dorpat, 1848) and Reichert (Müll. 'Arch,' 1847, Jahresbericht.) advise, it is well always to use only definite solutions. I may add, that a great saving of time is effected by the heating of the tissues to be investigated, in test tubes, with these and other reagents, as I have already done in examining those tissues of animals which contain cellulose ('Annales d. Sc. Nat.,' 1846).]

§ 46.

Growth and Regeneration.— The epidermis possesses no power of continually active growth depending upon intrinsic causes and founded upon the vital relations of its cells, or those which it has with the *corium;* it is essentially a stable tissue, which does not change in its elementary parts, but, somewhat like a cartilage,[1] has all its vital energies directed to its unchanged self-maintenance as a whole (thickness of the whole epidermis, proportion of the *rete Malpighii* to the horny layer), and in its separate parts. However, since a throwing-off of the external layers, if not necessarily, yet accidentally, takes place almost continually over the whole body to a greater

[1] [See, however, the note upon the desquamation of cartilage, *infra.*—Eds.]

or less extent, the epidermis is, so to speak, continually occupied in replacing what is lost, or in growing, and thus exhibits its vegetative life in a more remarkable manner. Whichever takes place, it is the *corium* and its vessels from which the fluids required by the epidermis are derived. In every locality, we may suppose, that a certain determinate quantity of plasma, corresponding with the anatomical and physiological relations of the vessels of the *corium* and the thickness of the epidermis, permeates the latter, and, when it is not growing, simply fills its cells and plates (independently of that more watery fluid which subserves the cutaneous evaporation), maintaining their vital activity, and at the most causing temporary deposits of pigment in the *rete Malpighii.* If, on the other hand, its outer layers be removed, a certain amount of plasma becomes free and disposable, and then regeneration takes place, which, if it proceed continuously, may even be called growth. It is in this process that the vegetative life of the epidermis-cells is most distinctly evidenced, particularly in the *rete Malpighii,* where it is unquestionably most intense, exhibiting itself especially, in the multiplication and growth of the cells, and in their chemical changes. In the horny stratum the phenomena are less striking, though it must not be considered to be inactive even in the uppermost layer; being by no means dead matter, as we evidently see, when under certain conditions, especially under abnormal states of the *corium*—the source of its nutrition—it sometimes becomes hypertrophied, sometimes completely dies away. We have not as yet, however, attained to an exact insight into the vital manifestations of the epidermic cells, and are therefore not in a condition to decide which of the phenomena presented by them are to be ascribed to their own activity, and which to the nature of the plasma which nourishes them. The latter is certainly of the greatest importance for the epidermis, and it is more than probable that most of its peculiarities, as, for instance, its typically different thickness in different parts of the body, the different relations of the *stratum Malpighii* to the horny layer, and its pathological states, depend upon qualitative and quantitative differences in the plasma. Upon what condition, furthermore, it depends, that in the Malpighian layer, the changes of the cells are far more considerable than in the horny layer, whose elements all closely

resemble one another, is as little obvious as the cause of the somewhat defined line of demarcation between the two layers, a condition which appears still more strikingly in the nails, and would lead one to suppose that, at the first formation and in the course of the development of the epidermis and nails, a very considerable alteration suddenly takes place at one point in their cells, thus determining their separation into two layers.

[In the deep fold of the skin which surrounds the *glans penis* and *clitoridis*, a continual desquamation and reproduction of the epidermic scales, which are here soft and nucleated, takes place, in consequence of which a peculiar secretion, the *smegma preputii*, is produced. Hitherto this secretion has been erroneously, but almost universally, supposed to be a sebaceous matter secreted by the preputial glands. The microscope shows: 1, that in the female, where the presence of *smegma preputii* is constant, neither sebaceous nor any other glands exist upon the prepuce or *glans clitoridis*; 2, that in the male, in whom such glands are indeed found, they are commonly but insignificant in relation to the quantity of *smegma*, and are often very few and scattered; 3, finally, that the *smegma*, in both sexes, consists principally of cells of the same form as those of the prepuce and *glans penis* and *clitoridis*; whence, taking also into account the fact, that in the male it is generally distinctly composed of superimposed layers covering the whole prepuce continuously, whilst the sebaceous glands occur only isolated, it naturally follows that the *smegma* is principally constituted of desquamated epidermis. However, this does not exclude the preputial sebaceous matter in the male from also taking a share in proportion to the number and size of Tyson's glands, in the formation of what goes under the common name of *smegma*. There would in this locality then, really be a constant desquamation of the external, and a new development of the internal layers of the epidermis, but here there are special purposes in view which elsewhere do not enter into consideration. The preputial fold, in fact, is to be compared to a gland; and as the secretions of these are very often formed only by the continual casting off of the cells which line them (*e. g.* sebaceous glands), so is that of the prepuce. We must recollect that in many animals *e. g.*, the Weasel, the Beaver (E. H. Weber), without essentially

changing the character which it possesses in man, the prepuce takes on a highly glandular nature, and that even in man it yields a secretion which differs considerably from common epidermis. According to Lehmann, the yellow, fatty, strongly-odorous preputial *smegma* of man contains, when dried, in 100 parts: Ethereal extract, 52·8; alcoholic extract, 7·4; aqueous extract, 6·1; earthy salts, 9·7; albuminous substances soluble in dilute acetic acid, 5·6; insoluble residuum, 18·5. The ethereal extract contained saponifiable fat, cholesterin, a non-saponifiable and uncrystallisable fat and bilin (Gallenstoff). The *smegma* of the horse possessed nearly the same constituents; and among the salts, oxalate of lime; while in man, ammonio-phosphate of magnesia occurred. The watery extract contained neither albumen nor casein.

An extensive desquamation of the entire horny layer of the epidermis, such as takes place in the embryo and in many animals, does not occur in man except in certain morbid states. On the other hand, its power of regeneration is exhibited in other modes than those which have been mentioned. Excised portions of the epidermis, for instance, are very readily replaced, and with tolerable rapidity, so long as the *corium* is not injured; and, in fact, not by the immediate deposition of epidermis in the wound, but only by the growing up of the whole epidermis from below. If the *corium* be injured as well, an epidermis is, indeed, formed upon the substance of the cicatrix, but without any of the previous elevations and depressions of the internal and external surface, because the new *corium* has neither papillæ nor ridges. If the epidermis be raised up into a vesicle by acrid substances, *e. g.*, *Tartar emetic*, a slight burn, &c., the wall of the vesicle, which consists of the horny layer and some few layers of cells of the mucous layer, never again becomes adherent; but from the main substance of the mucous layer, which mostly remains lying upon the papillæ, a new horny layer is by degrees developed.

If we inquire more minutely into the mode of regeneration of the epidermis, there can, in the first place, be no doubt that it takes place in the Malpighian layer, inasmuch as losses of substance of the horny layer, *e. g.*, a piece cut out, are restored not by the formation of a new portion in the gap, but by the growth outwards of a horny layer from below (the wound

remaining wholly unchanged), which gradually raises the bottom of the wound, and brings it to a level with the surrounding epidermis, the latter, in consequence of the pressure that it suffers from the growing portion, becoming everted and exfoliating. The reason of this phenomenon is to be sought, simply in this, that the non-vascular epidermis draws the materials which it requires for its nutrition and regeneration from the superficial vessels of the *corium*. It is more difficult to ascertain from what portion of the Malpighian layer the regeneration proceeds. If a layer of cyto-blastema and of free nuclei existed upon the surface of the *corium*, as many authors suppose, we might acquiesce in the view, that the epidermis grows by free cell-development in those innermost layers which rest immediately upon it; but such a cyto-blastema, as we have seen, does not exist, the *stratum Malpighii* being invariably formed by perfect cells; and thence nothing remains, but to suppose an endogenous cell-development around portions of contents in the deepest round cells, or a multiplication by division, for which latter view the occasional occurrence of two nuclei in some of the softer epidermic cells, seems to speak. It can be more easily made out, how, in the course of the growth of the epidermis, the youngest epidermic cells become changed into horny plates. The small and round vesicles of the deeper layers of the *stratum Malpighii* become larger and flatter the more they approach the surface, until at last they are completely converted into flattened plates. In the meanwhile their nuclei at first grow a little, and then, as a general rule, disappear wholly in the horny layer; whilst the cell-contents, which are granular in the mucous layer, clearly distinct from the cell-membrane, and probably semi-fluid, become more solid and homogeneous in the horny layer, and finally coalesce with the cell-membranes. At the same time the latter are chemically altered, becoming less and less soluble in caustic alkalies.]

§ 47.

Development of the Epidermis.—The first layers of the epidermis are developed, in the Mammalia, by the metamorphosis of the most superficial of the original formative cells which compose the young embryo. When the rudiments of the *stratum Malpighii* and horny layer are once indicated, the former con-

tinues to increase in thickness, in consequence of the multiplication of its elements, whilst the horny layer, for the increase of its proper substance and to replace what it loses by desquamation, recruits itself from it exactly as in the adult. How the multiplication of the cells goes on in the *rete Malpighii* has not been directly observed; but it is certainly not by free cell-development, since in embryos of all ages the mucous layer consists wholly of cells, and free nuclei are altogether absent. As regards the horizontal extension of the epidermis, it appears, as Harting ('Rech. micrométr,' p. 47) justly observes, from the circumstance that the epidermic scales of the fœtus and of the adult differ very little in superficial size, that it can only in a very slight degree be ascribed to the growth of its elements. In fact the horny plates of the embryo of fifteen weeks already measure 0·009—0·012''', in the sixth month 0·01—0·012''', in the seventh month 0·01—0·014''', in the new-born infant 0·012—0·016''', in the adult 0·008—0·016'''. Since, however, keeping in mind the structure of the horny layer, it cannot well be supposed that new scales are continually intercalated from below between its elements, and since a superficial multiplication of the cells of the *rete*, which also do not increase in size, must certainly be granted, it seems impossible to admit any other conclusion than that, in agreement with the great superficial growth of the cutis and of the *rete*, and the small extensibility of the horny layers, a series of desquamations of the latter take place, which, if this view be correct, must likewise obtain after birth.

[In an embryo of five weeks I found, in the place of the epidermis, nothing but an external layer of polygonal cells of 0·012—0·02''' in diameter, and an internal layer of small cells of 0·003—0·004'''; in embryos of fifteen weeks the epidermis is 0·01—0·012''', thick and composed as before, only that the deep layer of cells answering to the *stratum mucosum* is often already double, and the external cells measure only 0·009—0·012'''.

In the fifth month the epidermis in one instance measured on the heel and ball of the hand 0·02—0·024''', over the ridges of the cutis 0·036—0·04''', in the furrows between them on the back 0·02—0·024''', of which thickness one third may

be regarded as belonging to the horny layer and two thirds to the *rete Malpighii*. In a somewhat older embryo it was, on the heel 0·06—·064‴ (mucous layer 0·05, horny layer 0·01—0·014‴), on the surface of the hand 0·05‴ (mucous layer 0·04, horny layer 0·01‴), on the back 0·02—0·024‴ (mucous and horny layers of equal thickness). The mucous layers consisted of many layers of smaller cells, the lowest of which were already elongated, and stood perpendicularly; the horny layer, of at least two layers of polygonal flattened cells, with round nuclei.

In the sixth month the epidermis upon the thorax measures 0·02—0·022‴, on the palm of the hand 0·06‴, on the sole of the foot 0·07‴, and everywhere it consists of many layers of cells. The outermost one or two are composed of horny plates without nuclei 0·01—0·14‴ perfectly similar to those of the external horny layer in adults; then follow 3—4 layers of polygonal cells, the largest 0·01—0·012‴, with nuclei 0·004‴; finally a mucous layer, whose thickness equals about one half or two fifths that of the whole epidermis, with at least 3 or 4 layers of rounded cells of 0·003—0·004‴, the lowest of which are somewhat elongated, and are seated perpendicularly upon the cutis.

In the seventh month, I found in one embryo, that the epidermis on the heel measured 0·12‴ (mucous layer 0·072,‴ horny layer 0·048‴), upon the back 0·07‴ (mucous layer 0·04‴, horny layer 0·03‴): in another it measured on the heel 0·12—0·14‴ (mucous layer 0·05—0·06‴, horny layer 0·07—0·08‴), on the knee 0·046—0·064‴ (mucous layer 0·016—0·024‴, horny layer 0·03—0·04‴.) Both layers of the epidermis are as sharply separated from one another as in adults, and their elements similar to those of the perfect epidermis, especially the lowest parts of the *stratum Malpighii* and the plates of the horny layer, which have no nuclei, and measure 0·01—0·014‴ in the uppermost layers.

In the new-born infant, apart from the thickness of the epidermis, which in one case measured on the heel 0·1—0·11″ (mucous layer 0·04—0·05‴, horny layer 0·06‴) nothing particular is to be observed, except that by maceration, &c., it is much more easily separated from the *corium* than in the adult. The non-nucleated horny plates measured 0·012—·016‴, on the *labia minora* where they possess nuclei 0·016—0·02‴.

During embryonic life a desquamation of the epidermis occurs, which is perhaps repeated several times. Such is the fate, probably, of the layer of polygonal cells which arises first of all, and which in the second to the fourth months, becomes metamorphosed into an almost structureless membrane, and is then no longer to be found; perhaps also of the layer of epidermis, which covers the points of the hairs which have not yet appeared externally (*vide infra* § Hairs); and in the second half of the fœtal period it may be easily demonstrated as an actively occurring process. From the fifth month onwards, in fact, continually increasing desquamation of the external epidermic cells takes place, and these becoming in most parts mixed up with the sebaceous secretion of the skin, form the so-called *vernix caseosa* or *smegma embryonum*. This is a whitish or yellowish, viscid, inodorous material, which, especially from the sixth month onwards, covers the whole surface of the fœtus with an often considerably thick and even laminated substance, which is most abundant upon the *genitalia*, on the flexor side of the joints (axilla, knee, nates), on the sole, the palm, the back, the ear, and on the head in large quantity, and when microscopically examined consists mainly of epidermic cells, but also contains sebaceous cells and fat globules. According to Davy ('Lond. Med. Gaz.,' March, 1844) the *vernix caseosa* contains in 100 parts, 5·75 elain, 3·13 margarin (8·88 fat); the rest, 91·12 per cent., must be reckoned as epidermic scales, for since the *vernix caseosa* contains no free fluid, the 77·87 per cent. water and 13·25 solid substance found by Davy must be laid to the account of epidermic cells. This also holds good of Buek's analysis ('De Vernice caseosa,' Halis, 1844) who found in 100 parts, 10·15 fat, 5·40 epithelium, and 84·45 water (so that there was 89·85 of epithelium); and also in two other cases, in which the water was not exactly determined, he found 14·80 and 9·31 per cent. of fat, and therefore 86·20 to 89·69 of moist epithelium. According to Buek, the fat of the *vernix caseosa*, contains no cholesterin, as had been stated by Fromherz and Gugert, but oleic acid, and either stearic or margaric acid, which are probably not free, but combined with glycerine,—a circumstance which also evidences its origin from the sebaceous glands, in which, normally, no cholesterin is formed. Lehmann found (l. c.) in the dry *vernix caseosa* of a

nearly full-grown fœtus, 47·5 per cent. of ethereal extract, 15·0 of alcoholic extract, 3·3 of watery extract, 4·0 of acetic acid extract (earthy phosphates and albuminous substances), *epidermis* and *lanugo* 23·7. In the ethereal extract the reaction of bilin was absent and the fresh *vernix* contained a large quantity of water, which in all probability had entered its cells from the *liquor amnii.* The *smegma* generally appears about the sixth month, varies greatly in quantity, and is, especially in newly-born infants, sometimes very greatly developed (as much as $3\frac{1}{4}$ drachms, Buek), sometimes wholly wanting; in which latter case it either becomes mixed with the *liquor amnii,* which in fact often contains epidermic cells as well as fat (Mark, in Heller's 'Archiv,' 1845, p. 218), or may have been from the first, less developed. After birth the *smegma* is thrown off in the course of from two to three days, and the permanent epidermis appears, of whose further changes up to the adult state there is little to be said. In a child four months old the epidermis measured—

	Epidermis in toto.	*Rete Malp.*	*Horny layer.*
On the heel	0·26'''	0·12'''	0·14'''
On the back of the foot . .	0·048—0·06'''	0·032—0·04'''	0·016—0·02'''
On the palm	0·07—0·1'''	0·04—0·07'''	0·03'''
On the back of the fingers .	0·056—0·07'''	0·04—0·05'''	0·016—0·02'''

On comparing this with the adult, it is to be observed that the epidermis of the young child is disproportionately thick, and that this thickness depends especially upon the *rete Malpighii,* whilst the horny layer exhibits only a slight development. The pigment of the *rete Malpighii* arises, in the coloured races, only after birth. P. Camper ('Kleinere Schriften,' 1782, Bd. I, p. 24) saw a negro child, which at its birth was reddish, and hardly differed from that of an European, rapidly become tinged black at the edges of the nails and round the nipple. On the third day the *genitalia* became coloured, and on the fifth and sixth the blackness spread over the whole body. In Europeans also, at birth, the pigment of the *areola* and of the other places which have been mentioned is not yet present: it is gradually developed in the course of the first year, so that in children of two or three months old it is only indicated.

In investigating the skin, perpendicular and horizontal sections of fresh, dried, and boiled preparations are serviceable:

they may be moistened with an indifferent fluid or with various reagents, the most important points in regard to whose effects have been noticed in the foregoing paragraphs. The epidermis is separated from the *corium* by maceration, by boiling, and where it is not thick, as on the *genitalia*, by acetic acid and soda, easily and in large flakes, so that its lower surface and the papillæ of the *corium* become visible in the most beautiful manner, and the latter may be examined singly or in groups. In the fresh skin their position and number are quickly and easily to be recognised in horizontal sections, passing through the papillæ and the deep layers of the epidermis. Its vessels are to be studied in thin parts of the skin (*genitalia*, lips), in the fresh condition, or in injected preparations with those of the rest of the skin; its nerves in perpendicular sections, in isolated papillæ, or in thin portions of the skin (prepuce, *glans*, eyelids, *conjunctiva bulbi*) after the addition of acetic acid and dilute solution of caustic soda, or according to Gerber and Krause's method. Gerber boils the skin until it is transparent, lays it a few hours in oil of turpentine until the nerves are white and glistening, and then examines them in fine perpendicular sections made with the double knife. According to Krause, the nerves are seen very well after treating the skin with nitric acid, if the right amount of action is hit upon. The elastic tissue of the skin comes out well under the action of acetic acid, soda, and potass. The smooth muscles may be readily isolated in the *tunica dartos*—with more difficulty in the *penis* and in the *areola*, where it needs familiarity with them, in order in all cases, to recognise them with the naked eye. On the hair sacs they are rendered visible microscopically, if a sac, with the sebaceous glands which appertain to it, be isolated, especially after the application of acetic acid, as small bundles near and in front of the sebaceous glands, but best and very easily in perpendicular sections of boiled skin (Henle). The examination of the fat cells is especially instructive in thin persons, in whom their membranes and nuclei are readily visible: in other cases their membranes are readily demonstrable by the aid of ether, which extracts the fat; but the nuclei are seen with difficulty, though they may occasionally be discovered here and there even in full cells. The epidermis must, for its Malpighian layer especially, be examined fresh, in fine perpendicular sec-

tions, to which acetic acid and dilute solution of soda may be added; the horny layer, particularly by the addition of alkalies, in perpendicular and horizontal sections; however, mere maceration in water separates its elements from one another, and those who are practised can discover them in fresh preparations, when viewed both laterally and from the surface.]

Literature.—Gurlt, 'Vergleichende Unters. über die Haut des Menschen u. d. Haus-säugethiere,' &c. in Müll. 'Archiv,' 1835, p. 399 (good figures for the period); Raschkow, 'Meletemata circa Mammal. dentium evolutionem,' Vratisl, 1835 (first more complete description of the elements of the epidermis under Purkinje's guidance); Simon, 'Ueber die Structur der Warzen u. über Pigmentbildung in der Haut,' Müll. 'Arch.,' 1840, p. 167 (pigment-cells in the *rete* of white persons); Krause, article 'Haut,' in Wagner's 'Handwörterbuch,' II, 1844, p. 127 (a detailed and excellent treatise); Kölliker, 'Zur Entwicklungsgeschichte der äussern Haut,' in 'Zeitschrift für wiss. Zool.,' Bd. II, p. 67; 'Histological Observations,' ibid. II, p. 118; Eylandt, 'De musculis organicis in cute humanâ obviis,' Dorp. Liv., 1850. Besides these, refer particularly to the works of Simon ('Die Hautkrankheiten durch anatomische Untersuchungen erläutert,' 2 Aufl., Berl., 1851); Von Bärensprung ('Beiträge zur Anat. u. Pathol. der menschlichen Haut,' 1848); and Krämer ('Ueber Condylome u. Warzen,' Götting., 1847). Figures are given by R. Wagner, 'Icon. phys.;' Berres, tab. vi, vii, xxiv (middling, with the exception of what regards the vessels); Arnold, 'Icones org. sens.,' tab. xi (very pretty, but drawn with too low magnifying powers); Hassall, tab. xxiv, xxvi, xxvii (among others, the skin of the negro also, and the areola of the white from within, coloured); and myself, 'Mikr. Anatomie,' Taf. i.

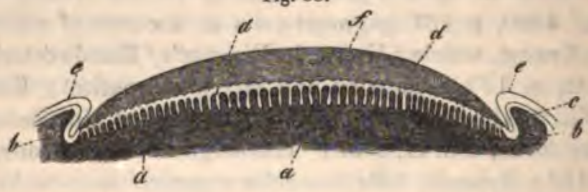
II.—OF THE NAILS.

§ 48.

The *nails, ungues,* are nothing but *peculiarly metamorphosed parts of the epidermis,* and like it, they consist of two layers,—of a soft *mucous-*, and a *horny layer*, or *the proper nail.*

That part of the *corium* upon which the nail lies, or the *bed of the nail*, corresponds exactly in form with it, is elongated, quadrangular, arched in the middle, shelving off anteriorly and posteriorly, and especially on the sides. When the nail is removed by maceration in connection with the epidermis, its anterior and middle parts are uncovered, whilst its lateral edges and its posterior segment, on the other hand, are invested by a process of the *cutis*, the *wall of the nail*, which is anteriorly depressed and rounded off, posteriorly more acute and longer, and, taken together with the *bed*, forms a fold, the *fold of the nail*, which receives the lateral edges and the posterior (2—3‴) portion of its root (figs. 58, 60).

Fig. 58.



The *bed of the nail* presents upon its surface peculiar *ridges*, similar to those of the palm and of the sole of the foot (fig. 58 *a*). They begin at the bottom of the fold of the nail, at the posterior border of its bed, and, as Henle (p. 270) justly remarks, they run from the middle of it almost as from a pole. The middle ones pass directly forwards; the lateral at first describe an arc, which is the more convex the further out the ridges lie, and eventually are directed forwards like the others. At a distance of $2\frac{1}{2}$—$3\frac{1}{2}$‴ from their origin, they all at once become more prominent, and take on the form of true *laminæ*, of 0·024—0·1‴ in depth, which run directly, almost to the anterior edge of the bed of the nail, and then end suddenly, as if truncated. The line of transition of the ridges into the *laminæ* is convex anteriorly, and divides the bed of the nail into two sections, differing both in their extent and in their colour: the posterior smaller one is nearly covered by the

Fig. 58. Transverse section through the body and bed of the nail, × 8: *a*, bed of the nail, with its ridges (black); *b*, *corium* of the lateral parts of the wall of the nail; *c*, *stratum Malpighii* of the nail with its ridges (white); *e*, horny layer on the wall of the nail; *f*, horny layer of the nail, or proper nail substance, with short notches upon its under surface.

wall of the nail and underlies its root, the anterior and reddish-coloured division underlying its body. The ridges and laminæ of the bed of the nail, the number of which varies between 50 and 90, are, at their edges, beset with a series of short papillæ of 0·008—0·016‴. In addition, I can confirm Henle's statement that the bottom of the fold of the nail exhibits a few transverse ridges with larger papillæ directed forwards; further forwards, where the *laminæ* cease, there are also long isolated papillæ. On the nail of the little toe, the papillæ are frequently not seated upon ridges, but are more dispersed.

The *wall of the nail* has no ridges upon its lower surface, and rarely a papilla here and there. These commence again upon its margin, where they are of some length, and are continued thence upon its upper surface, which is in no respect distinguishable from the *cutis* of the back of the fingers and toes.

Fig. 59.

The *corium* of the wall and of the bed of the nail is dense, and for a considerable distance contains but little fat; in the ridges and laminæ with their papillæ, it is abundantly provided with fine elastic fibres. The vessels are particularly numerous in the anterior segment of the bed of the nail; behind, where the root of the nail lies, and in the wall they are more scanty; their capillaries, 0·005 — 0·008‴, form very distinct simple loops in the papillæ, and single trunks often pass, even into many papillæ. The *nerves* have the same relations below as in the skin, but I have hitherto been unable to detect either terminal loops or divisions in them.

In the nail itself we may distinguish, the *root*, the *body*, and the *free edge* (fig. 60). The soft root (fig. 60 *l*) corresponds in its extent to the posterior ridged segment of the bed of the nail, and is either wholly hidden in the fold, or exposes a small semi-lunar surface, the *lunula*. The posterior edge is attenuated, slightly bent upwards, and is the thinnest and most flexible part of the nail. The hard *body*, which increases in thickness and breadth from behind forwards (*k*), lies for the most part with its upper surface un-

Fig. 59. Capillaries of the bed of the nail, after Berres.

covered; its somewhat sharp thin edges are hidden in the lateral parts of the fold, and its under surface reposes upon

Fig. 60.

the anterior segment of the bed of the nail: lastly, the free edge (*m*) is, in cut nails, directed straight forwards, but if uncut, it curves downwards round the ball of the finger, and with the rest of the nail, attains to a length of as much as two inches.

The lower surface of the *body* and of the *root* answer in their form exactly to the bed of the nail, and we therefore find laminæ and ridges upon them, as well as furrows, in the same order as on the latter, only here the edges of the laminæ are straight and not papillated, whilst the furrows, instead of having an even bottom, as in the nail-bed, are provided with shallow pits for the reception of the papillæ. By the mutual inter-locking of the elevations and depressions, the intimate union of the nail with the *corium* is effected, which becomes still more close by the application of the under surface of the wall of the nail upon its base and edges.

The colour of the nail, so long as it remains in its natural condition, is whitish and transparent, at its free edges; reddish in the body, with the exception of a very narrow clear margin close behind the commencement of the free edge; in the *lunula*, whitish; the colour of the last two portions arising principally from the *corium* and its blood-vessels which shine through them. Separated from the *corium* and epidermis, the

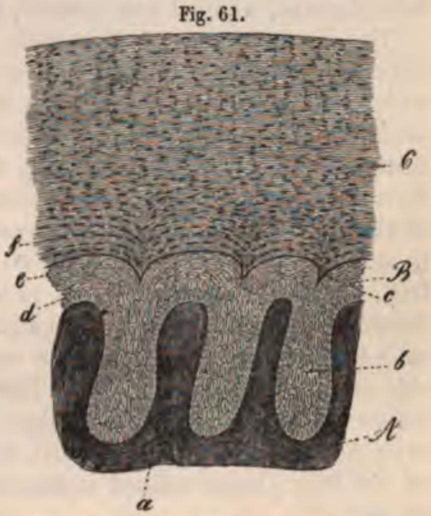
Fig. 60. Longitudinal section through the middle of the nail and bed of the nail, × 8: *a*, bed of the nail, and cutis of the back and points of the fingers; *b*, mucous layer of the points of the fingers; *c*, of the nail; *d*, of the bottom of the fold of the nail; *e*, of the back of the finger; *f*, horny layer of the points of the fingers; *g*, beginning of them under the edge of the nail; *h*, horny layer of the back of the fingers; *i*, ends of it upon the upper surface of the root of the nail; *k*, body; *l*, root; *m*, free edge of the proper substance of the nail.

nail is of a tolerably uniform whitish colour, and transparent, though somewhat whiter at the root than in the body.

§ 49.

Structure of the Nail.—The nail consists in its deeper parts of a soft, somewhat pale *stratum mucosum*, which is distinguished from the hard external horny layer, or proper nail, still more sharply than in the common epidermis. It covers the whole of the lower surface of the root and body of the nail, frequently also a small part of the upper surface of the root, and forms by itself the above-mentioned laminæ on the under surface of the nail. Its thickness at the posterior part of the root upon the under side measures 0·12‴; on the upper, 0·14‴; close behind the margin of the root directly from behind forwards, 0·24—0·26‴; on the body of the nail on the laminæ, more posteriorly and at the edge 0·04—0·05‴; in the middle 0·06‴, even 0·08—·096‴ and 0·12‴; between these, 0·032—0·04‴.

Fig. 61.



The Malpighian layer of the nail, like that of the epidermis, consists wholly of nucleated cells, and agrees in all essential points with it, except that the deep portion contains many layers of elongated (of 0·004—0·007‴) perpendicular cells, in consequence of which a striated appearance is produced, which has

Fig. 61. Transverse section through the body of the nail, × 250. *A*, *cutis* of the bed of the nail; *B*, mucous layer of the nail; *C*, horny layer of it, or proper nail substance: *a*, layers of the bed of the nail; *b*, layers of the *stratum Malpighii* of the nail; *c*, ridges of the proper substance of the nail; *d*, deepest perpendicular cells of the mucous layer of the nail; *e*, upper flat cells of it; *f*, nuclei of the proper substance of the nail.

misled Günther, and probably Rainey also,[1] into supposing the existence of peculiar glands under the nail. In the Negro, according to Béclard (Anat. Générale, p. 309), the *stratum Malpighii* of the nail is black; and according to Krause (l. c., p. 124), its cells would in this case appear to contain dark-brown nuclei, as well as yellowish-brown ones, in dark Europeans. According to Hassall (p. 252), the younger cells of the nail (*i. e.*, those of the *stratum mucosum*), generally contain pigment, which I can confirm, at least in some cases.

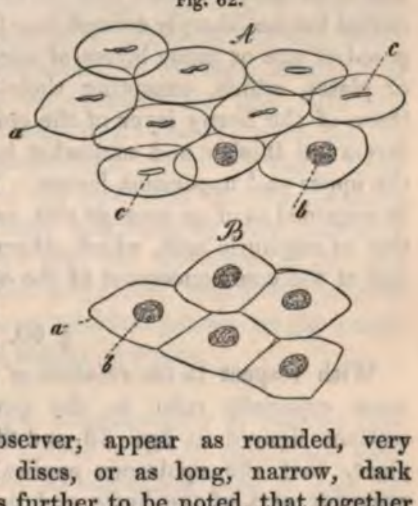
The *horny layer* of the nail, or its proper substance (figs. 58 *f;* 60 *k, l, m;* 61 *c*), is that hard brittle portion which forms its upper part and its free edge. The under surface of this layer is quite smooth, posteriorly at the root; further forwards it exhibits sharp ridges separated by broad furrows, which are inserted into the furrows of the mucous layer of the nail. These ridges of the proper nail substance appear in transverse sections (figs. 58, 61), as pointed processes of 0·01—0·02‴ in length, which, as a rule, are most strongly developed at the edges of the nail, even to 0·04—0·06‴, and answer precisely in their number to the laminæ of the under side of the *stratum Malpighii.* The upper surface of the substance of the nail is smooth, taken as a whole, yet sometimes even here, very distinct, parallel, longitudinal streaks appear as the last, almost effaced indications, of the inequalities of its bed.

Usually, the thickness of this part of the nail continually increases from the root to near the free edge, so that the body of the nail is, anteriorly, at least three times thicker (from 0·3—0·4‴) than the former; at the free edge, again, it becomes somewhat less. In its transverse diameter also, with the exception of the posterior edge of the root, the substance of the nail is not everywhere equally thick; it thins considerably towards the lateral edges, so that at last the nails, where they lie in the fold, measure not more than 0·06—0·12‴, and finally terminate quite sharply.

[1] [With respect to Rainey's observations, Reichert, in his Report for 1849-50 ('Müll. Arch.,' 1850-51), says that the observation as to the follicles is quite correct, and that with Dr. Ammons, who had studied the growth and regeneration of the nails for some years, he had seen such capsules containing horny cells, with especial distinctness upon the bed of the nail of the great toe.—Eds.]

With regard to the structure of the proper substance of the nail, it can hardly be made out without the action of reagents. In perpendicular sections we see, particularly in the body, nothing but horizontal, fine, straight, or curved, closely approximated lines, which one would be inclined to consider as the optical expression of delicate, super-imposed lamellæ, and between these, a multitude of elongated, horizontal, opaque or peculiar reddish-transparent striæ, evidently nuclei. Only upon the most posterior part of the root, and on the under surface, where it meets the *stratum Malpighii*, do more or less distinctly flattened cells with nuclei appear disposed in layers. Horizontal sections show even less than the perpendicular ones; exhibiting a pale transparent substance, granular here and there, and mostly without indication of any structure whatsoever, occasionally with very indistinct contours of plates similar to those of the horny layer of the epidermis. Very different are the appearances presented after treating the nail with alkalies and certain acids.

Fig. 62.



If the substance of the nail be boiled in dilute caustic soda, it becomes changed upon the first bubbling of the fluid into a beautiful cellular tissue (fig. 62, *A*, *B*), whose polygonal elements all, without exception, the deep as well as the superficial, possess nuclei of 0·0030—0·0046‴ in length and breadth, and 0·002‴ in thickness, which, according as they turn their surfaces or their edges to the observer, appear as rounded, very pale, and finely-granulated discs, or as long, narrow, dark contoured rods; it deserves further to be noted, that together with these, large and very pale nuclei of 0·006—0·01‴ and more, occur in considerable numbers, probably owing their existence to the excessive action of the reagent which has

Fig. 62. Nail plates boiled with caustic soda, × 350. *A*, from the side; *B*, from the surface: *a*, membranes of the distended elements of the nail; *b*, their nuclei, from the surface; *c*, from the side.

swollen them up. Caustic soda and potass also (which has a similar action upon the whole, though it acts more upon the nuclei) demonstrate the important fact, that the cells of the nail are flatter in the superficial, than in the deeper layers. If, in fact, a fine perpendicular section be moistened with cold, or better, with hot solution of soda, we see the cellular structure of the nail appear almost at the very instant it becomes moistened, without any obvious enlargement of its elements; and it is observable, at the same time, that its deepest cells are at least as thick again as the most superficial.

If the soda solution acts longer, the section gradually swells up, in the under cells first, on account of their greater softness, and only subsequently in the flat and hard upper elements. By treating the nail with cold sulphuric and nitric acids, and also by boiling with hydrochloric acid, its elements are isolated.

Taking these facts, together with what we see in the unaltered nail, it results that its horny layer consists of closely united but not sharply defined lamellæ; each lamella being composed of one or many layers of nucleated, polygonal, flat scales or plates, which, excepting their nuclei, are very similar to those of the horny layer of the epidermis and in their deepest layers are thicker and somewhat less in circumference than in the upper and uppermost layers. Those of 0·012—0·016‴ may be regarded as of an average size, as may be seen upon the addition of sulphuric acid, which otherwise exerts but little action, and at the commencement of the operation of soda and potass.

§ 50.

With respect to *the relation of the nail to the epidermis*, I must especially refer to the perpendicular and transverse sections figured in figs. 58 and 60. They show, in the first place, that the epidermis applies itself upon the root, the posterior part of the body, and upon the margins of the nail, and that it meets it under the free edge and on the anterior parts of the lateral edges. This happens in such a manner, that whilst the mucous layer of the epidermis passes continuously and without any line of demarcation, into that of the nail, the horny layer is, properly speaking, never continued directly into the actual substance of the nail, but partly applies

itself with its lamellæ parallel upon the nail, partly abuts upon it at various oblique angles. At the root, the horny layer passes more or less deeply into the fold of the nail, and at the same time runs, in a thin layer which becomes very fine anteriorly, upon the upper free part of the nail, as far as the end of the *lunula* or the beginning of the body. Anteriorly and posteriorly, in which latter region this layer not uncommonly reaches the posterior margin of the root, its cells lie parallel to the upper surface of the nail; while in the middle, where it is thickest (fig. 60 *i*), they are oblique or perpendicular to it. At the free edge of the nail the relations of the parts are similar, where the horny layer meeting the end of the under surface of the body of the nail, partly with more horizontal, partly with oblique lamellæ, is perhaps also continued upon the commencement of the free edge. On the lateral edges, again, the horny layer passes anteriorly, in horizontal strata, under the nail; more posteriorly it is arranged as upon the root, or simply rests against the edge of the nail. The horny layer thus forms a kind of sheath for the nail, which bears some resemblance to the sheath of the hair, though it is much more imperfect. If we compare the nail with the epidermis, we find, in the structure of its mucous layer, not the slightest peculiarity of any importance, while the horny layer is distinguished from that of the epidermis by its cells being nucleated, harder, and chemically different; by their flattening and intimate union. For the rest, the agreement of the two structures is so close, that the proper nail may justly be considered, as it has long been, a modified portion of the horny layer of the last joints of the fingers and toes.

[According to the chemical investigations of Scherer and Mulder, the nails agree very closely with the epidermis; and, according to Mulder, they are distinguished from it, only by their somewhat greater proportion of sulphur and carbon. In his last essay, he considers them to be composed of protein + sulphamid (6·8 per cent. of the latter). This agrees with the observed action of reagents, with which the plates of the nail behave almost exactly like horny plates, only they are attacked with more difficulty and possess nuclei. According to Lauth, the nails contain more phosphate of lime

than the epidermis, whence they derive their hardness: this may be correct, although, as Mulder states ('Phys. Chemie,' p. 536), both yield about the same proportion of ash (1 per cent.).

As regards the lamellar structure of the proper nail, it is to be regarded in the same light as that of the horny layer of the epidermis; but it is not so distinct, because the plates of the nail are more intimately connected than the elements of the epidermis. Reagents, however, render the lamellar structure very evident, and it is also clear in pathologically thickened and curved nails.

§ 51.

Growth of the Nails.—The nails grow continually, as long as they are cut; on the other hand, if uncut, their growth is limited. In this case, as may be observed in those who are long confined to their bed by sickness, and in the Eastern Asiatics, the nails become $1\frac{1}{2}$—2 inches long (in the Chinese, according to Hamilton, 2 inches), and curve round the points of the fingers and toes.

During the growth of the nail, the mucous layer does not change its position at all, but its horny layer is constantly being thrust forward. The formation of the latter goes on continually wherever it is in contact with the *stratum Malpighii,* in other words upon its whole under surface, with the exception of the free anterior edge; further, in many nails, upon a very small portion of the upper surface of the root, finally, at the posterior edge of the root itself. It is, however, the root portion which grows fastest, whilst the body of the nail is more slowly developed, which is demonstrated especially by the fact that it is not much thinner at the boundary between the root and the body than it is anteriorly upon the body itself, and that the transition of the cells of the *stratum Malpighii* into nail-cells is easily shown at the root, but with difficulty in the body. By the constant addition of new cells at the edge of the root, the nail grows forwards; by their addition to its under surface, it is thickened. The longitudinal growth exceeds that in thickness, because the first rounded cells, as they move from behind and below, forwards and upwards, become more and more flattened and elongated.

[The mode in which the plates of the nail arise from the cells of the mucous layer, is easily demonstrable at the root of the nail. Here, in fact, the uppermost cells of the mucous layer are constructed very differently from the deeper ones; they are more or less flattened, and closely resemble the cells of the epidermis, but they possess a nucleus, which, however, is only to be discovered by adding caustic soda, and then with difficulty. If we follow these cells, which form a layer of 0·06—0·12‴ in thickness, towards the proper substance of the nail, we find that they become more and more flattened, and at last pass without any defined boundary into the latter, uniting together more closely, and taking on a more transparent appearance.

In the *body of the nail*, the formation of nail substance is demonstrated with more difficulty, yet here, in opposition to Reichert, we must assume that it does take place, because the nail almost invariably increases in thickness even in the body, from behind forwards. However, there is unquestionably, in this part, a sharper demarcation between the two layers of the nail, than in the root; but in fine sections it appears by no means so sharp as in those which are commonly examined, and I find, in fact, that the transition of the cells of the mucous layer into the plates upon the body of the nail, is demonstrable with tolerable readiness, particularly on the addition of alkalies, where the ridges of the under surface of the proper nail are well developed. Between the ridges also, though no direct transition is recognisable, yet it may be observed that the plates of the proper nail which border upon the mucous layer are much less flattened than in the interior and on the surface, which also indicates that they are developed upon the spot. In conclusion I must add, in support of my view, that it is only in this way, that it becomes explicable why the under surface of the proper nail substance upon the root of the nail is almost smooth, while on the body of the nail it presents more or less prominent ridges. The origin or increase of these ridges demonstrates clearly that nail-substance is also formed here. Corresponding with these ridges and with the grooves between them, we also find that the lowest layers of the nail plates, which are quite horizontal upon the root, run with an undulating course upon the body (fig. 61). The general result then is, that whilst the formation

of the nail goes on especially at its root, yet that plates are added to the body of the nail from below, though more slowly and scantily, thus producing the anterior thickening, or at least preventing the necessary thinning of the nail anteriorly. It is to be remarked further, that the development of nail-substance takes place in all parts of the middle line of the nail more rapidly than in the lateral portions, which, anteriorly, are almost as thin as in the root, though they possess longer processes below. But even there, substance must be added to the body of the nail, because it becomes broader anteriorly.

The plates of the substance of the nail once formed, alter in certain respects, as they are pushed forwards and upwards by those which come after them. In the first place, their nature becomes altered in a manner which is little understood, the change consisting partly in the deposition of more phosphate of lime, partly in a solidification (conversion into horn) of their organic elements, particularly of the cell-membranes, in consequence of which, from being soft, as at the root and under surface of the nail, they become gradually harder and harder. In the second place, like the horny cells of the epidermis, they are very considerably flattened, and at the same time increase somewhat in their longitudinal and transverse diameters; finally, they coalesce more completely, so that they cannot be separately recognised, without the action of reagents, in the upper and anterior parts of the nail, which appear to be composed of nothing but a homogeneous substance which tears in all directions; whilst in the lower parts the separate nail-plates are, at least indicated, and are occasionally tolerably distinct. On the other hand, the nuclei of the nail-plates do not disappear, and in this lies a characteristic distinction between the horny layer of the nail and that of the epidermis. They are to be seen in perpendicular sections, of fresh nails, and after treatment with caustic soda, and even in the most superficial layers, though somewhat smaller and flatter than in the deep layer. It follows then, that certain metamorphoses go on in the proper substance of the nail, which as in the epidermis, are to be ascribed to a peculiar growth and vital process in the nail-cells themselves. These seem to occur, however, almost solely in the lower and posterior parts of the nail, for if, as Schwann states (fig. 91), two points be marked upon the posterior portion of the free

surface of the nail, one behind the other, by piercing it with a needle and colouring with nitrate of silver, they in no wise alter their relative position in the course of the two or three months, during which they are moving towards the point of the nail.

As to the *pathological conditions* of the nails, they are readily regenerated when they have been detached, in consequence of crushing, burning, freezing, cutaneous disorders (scarlet fever, &c.), inflammations, exudations, suppurations and effusions of blood in the bed of the nail; in fact, as Pechlin ('Obs. Phys. Med.,' p. 315) narrates, this regeneration may take place periodically; in a boy, the nails, every autumn became blueish-black and desquamated, together with the epidermis (the horny layer ?), and were subsequently regenerated. In such a case, according to Lauth ('Mém. sur divers points d'Anatomie,' in the 'Annales de la Société d'Histoire naturelle de Strasbourg,' t. i, 1834), and Hyrtl ('Anatomie' p. 382), the whole bed of the nail becomes covered by soft horny plates, which harden by degrees, grow into a regular nail, and eventually project with their free edges beyond the end of the finger. When the last joint of the finger has been lost, rudimentary nails frequently appear upon the back of the second and even of the first phalanx. The older cases are quoted in Pauli ('De vulneribus sanandis,' Gottingæ, 1825, p. 98), more recently Hyrtl (l. c.) saw such a nail 2‴ long and 3‴ broad on the first phalanx of the thumb. As the formation of nail-substance depends upon the vessels of the bed of the nail, we may, with Henle, assume that varying conditions of the latter may frequently produce local thickening, thinning, or even detachment of the nail, and that their deformities in cyanosis and phthisis depend on these causes. The thickening and abnormal development of the nails, however, arise very frequently, as I have observed, from a partial obstruction of the capillaries of their bed. Thus in the lamellated nails of old people, greatly thickened and curved downwards in front, I find all the capillaries of the anterior segment of the bed of the nail closely filled with fat granules of different sizes, and wholly impermeable to the blood; in such a case the development of nail-substance can take place only in small lamellæ in the fold, which then, as may be readily understood, are raised up by those which are growing behind into a con-

tinually more and more oblique position; their posterior extremities forming, on the surface of the nail, transverse streaks one behind another at short intervals. After dividing the *nervus ischiadicus,* Steinrück ('De nervorum regeneratione,' pp. 45—49) observed, in the Rabbit, that the nails and hair fell off, which is a result of the influence of the nerves upon the vessels. Finally, the shape of the bed of the nail also influences its formation. It is thus explained, how (see Henle, l. c.), after inflammation and closure of the fold of the nail, the formation of new nail at the posterior edge ceases, the nail no longer growing forwards, but at all its edges exactly covering its bed.

§ 52.

The *development* of the nail begins in the third month with the formation of the bed and fold, which are marked off from the surrounding parts by the gradual growth of the skin into the wall of the nail. At first the bed of the nail is lined by the same cells as those which form the other parts of the epidermis (see § 47), only that even in the third month the cells of the *stratum Malpighii* are distinguished by their elongated and polygonal form (length 0·004‴; breadth 0·001—0·0016‴). In the fourth month there arises, between the *stratum Malpighii* and the horny layer of the bed of the nail, which latter is formed by a simple layer of polygonal clearly nucleated cells, a simple lamina of pale, flat, but also quadrangular and nucleated cells, 0·009‴ in diameter, which are closely united together, and must be regarded as the first indication of the proper substance of the nail; at the same time also, the *stratum Malpighii* under these cells becomes thickened so that it is certainly composed of, at least, two layers. The nail is therefore *at first wholly included within the epidermis;* it is formed over *the whole surface of the bed of the nail* as a quadrangular plate, and arises between the embryonic mucous layer and the horny layer, without doubt by a metamorphosis of the cells of the mucous layer, as is probable especially from the minute size of the original cells of the nails. In the course of its further development, the nail is thickened by the addition of new cells from below (in the fifth month its thickness is about 0·024‴, in the sixth 0·04‴, of which in the latter 0·025‴ must

be reckoned as proper nail substance); it increases by the extension of its elements and by the addition of new ones at its edges; but it remains even to the end of the fifth month, hidden under the horny layer of the epidermis, until finally it becomes free, and in the seventh month, even begins to grow longitudinally, so that at this period, except in its greater softness and its smaller dimensions, it presents no essential difference from the perfect nail. With regard to the bed of the nail, its ridges are already indicated at the end of the fourth month, and in the fifth they are well marked, 0·02—0·024‴ deep, 0·004—0·005‴ broad, and 0·008—0·014‴ distant; these measurements also indicate the breadth of the laminæ of the *stratum Malpighii*. At the sixth month they are somewhat larger and further apart.

In the new-born infant, the whole nail is 0·3—0·34‴ thick; 0·16‴ being proper nail substance, 0·14—0·18‴ *stratum Malpighii*. Its elements are still almost identical with those at the sixth month, and they appear with tolerable distinctness in the nail proper without any reagents, as elongated polygonal nucleated plates 0·02—0·028‴, as Schwann has already partly remarked. The free edge, projecting far forwards, which is presented in all nails, is worthy of remark. It is considerably thinner and narrower than the body, and is separated from it by a semilunar line; it is rounded anteriorly, as much as 2‴ long, and is plainly nothing but the nail of an earlier period which has been thrust forward by the longitudinal growth of the nail in the course of its development. In fact it nearly corresponds in size with a nail of the sixth month.

Soon after birth the long free edge of the nail of the new-born infant is cast off, at least once (according to Weber many times), in all probability in consequence of external mechanical violence, which it is unable, owing to its delicacy, to resist. In the sixth and seventh months after birth, I find that the nails which the child brought into the world, are completely replaced by new ones, and in the second and third years the nail-plates are not distinguishable from those of the adult, whence it follows that the nail increases in thickness, less in consequence of any enlargement of its elements, than by the addition of new ones to its edges and under-surface.

[The investigation of the nail-cells and plates is best made in fine sections of recent nails, with and without the addition of reagents, especially caustic soda and sulphuric acid, concerning whose operation the most important points have already been noted. To examine the relations of the parts of the nail to one another and to the epidermis, the nails must be separated from the *cutis* by maceration, or by boiling in water. It is then seen, that the nail is detached, with the cuticle, from the finger; and in transverse and longitudinal sections, its mode of connection with the former is perceived. The bed of the nail also, its *laminæ* and ridges, the fold and the *laminæ* in the *stratum Malpighii* of the nail, are easily seen, in this way. Since fine sections, in such a nail, are not readily made, precisely in the most important parts—the margins and root,—it is necessary, for this purpose, to employ fresh nails separated from the bone with the *cutis*, and dried. These afford all the information required, portions of them swelling up readily in water, and exhibiting the structure of the different layers, with acetic acid and caustic soda, in the most distinct manner.]

Literature.—A. Lauth, 'Sur la disposition des ongles et des poils,' Mem. de la Société d'hist. nat. de Strasbourg, 1830-4; Gurlt, 'Ueber die hornigen Gebilde des Menschen u. der Haussäugethiere,' Müll. 'Arch.,' 1836, p. 262; Reichert, in Müll. 'Arch.,' 1841, Jahresbericht; O. Kohlrausch, 'Recension von Henle's allgem. Anat.,' in Götting. 'Anzeigen,' 1843, p. 24; Rainey, 'On the structure and formation of the nails of the fingers and toes,' in 'Trans. of Microsc. Society,' March, 1849;' Berthold, 'Beobachtungen über das quantitative Verhältniss der Nägel- u. Haarbildung beim Menschen, in Müll. 'Arch.,' 1850.

III.—OF THE HAIRS.

§ 53.

In every hair we distinguish the free part or shaft, *scapus*, with its tapering point, from the portion inclosed within the sac, the root, *radix*. In straight hairs the former is generally straight and rounded; in the wavy, undulated and somewhat flattened; in the curly and woolly hairs, it is twisted spirally and quite flat or slightly ribbed. The root is always straight, tolerably cylindrical, and softer and thicker than the shaft, at

least in its lower part; in living hairs it ends in a still softer knob-like enlargement, $1\frac{1}{2}$ to 3 times thicker than the shaft,—the "bulb of the hair" (*c*), which is placed, cap-like, upon a papillary process of the sac, the "hair-papilla" (less properly termed *pulpa*, or *blastema pili*, hair-germ), or, in other words, receives the papilla in an excavation in its base.

Fig. 63.

§ 54.

Disposition and size of the Hairs.—The hairs are distributed over almost the whole surface of the body,[1] but exhibit very considerable differences in size and number, according to their situation, to individual peculiarity, age, sex, and race. As regards the former, three varieties may be admitted, besides many transitional forms: (1) long soft hairs, of 1′—3′ and more in length, 0·02—0·05‴ in thickness; (2) short stiff thick hairs, of $\frac{1}{4}$—$\frac{1}{2}$″ in length, and 0·03—0·07‴ in thickness; (3) short, excessively-fine hairs, down (*lanugo*), of 1—6‴ in length, and 0·006—0·01‴ in thickness. The distribution of the first form is well known; to the second belong the hairs at the entrance of the nostrils (*vibrissæ*), in the external auditory passage, the eyelashes (*cilia*), and eyebrows; to the third, finally, must be referred

Fig. 63. Hair and hair sacs of middling size, × 50: *a*, hair shaft; *b*, root of the hair; *c*, bulb of the hair; *d*, epidermis of the hair; *e*, inner root-sheath; *f*, outer root-sheath; *g*, structureless membrane of the hair sac; *h*, transversely and longitudinal fibrous layer thereof; *i*, papilla of the hair; *k*, excretory ducts of the sebaceous glands, with epithelium and layers of fibres; *l*, cutis at the aperture of the hair sac; *m*, stratum mucosum; *n*, horny layer of the epidermis, the latter somewhat retracted into the sac; *o*, end of the inner root-sheath.

[1] [No hairs exist upon the upper eyelids, the lips, the palm of the hand, and sole of the foot; nor on the dorsum of the last joints of the fingers and toes, the inner surface of the prepuce, and the glans penis.—Eds.]

the hairs on the face, trunk, and extremities, also those of the *caruncula lachrymalis*, and those (frequently absent) of the *labia minora* (Henle).

The number of hairs upon a given extent of surface varies very much, depending especially upon age, sex, and the colour of the hairs. According to Withof, on a surface of $\frac{1}{4}\square''$ there were found 147 black, 162 brown, 182 fair hairs. In a moderately hairy man, he found on $\frac{1}{4}\square''$ 293 upon the scalp, 39 on the chin, 34 on the pubis, 23 on the fore arm, 19 upon the outer margin of the back of the hand, 13 on the anterior surface of the leg. In men, closely set hairs occur not unfrequently upon the chest, shoulders, and extremities.

The hairs are placed either singly, or in twos and threes, even four and five together. The latter is the rule in the fœtus, but the same disposition obtains also in adults, especially in the *lanugo*. As Osiander and especially Eschricht, have shown, the direction of the hairs and hair-sacs is rarely straight, but oblique, and in different degrees in different parts of the body, as may be demonstrated with ease in the hairs of embryos, and, though less obviously, in adults also. The regularity depends on this, that the hairs being arranged in curved lines, which converge towards either certain points or certain lines, or diverge from them in two or more directions; there result a multitude of figures, which may with Eschricht be denominated "streams," "whorls," and "crosses." Streams with converging hairs are found, for example, in the median line of the back, chest, and abdomen, in the line which answers to the ridge of the tibia, &c. &c.; streams with diverging hairs occur on the line between the thorax and abdomen, on the one hand, and the back on the other, &c.; whorls and crosses with diverging hairs are found in the axilla, on the scalp, at the internal angle of the eye; with converging hairs, on the elbow. For further details I must refer to Eschricht's figures and descriptions, concerning which, however, it is to be remarked, that many variations occur with regard to these points, and Eschricht's figures represent only some of them.

§ 55.

External peculiarities and chemical composition of the Hairs. In embryos, the hairs are generally quite colourless and clear;

they very slowly become coloured, so that in youth they are, in general, paler than in middle age. In the adult the downy hairs, which have remained in a fœtal condition as it were, are invariably the palest; the longer ones are always darker, and the darkest are those of the head, beard, and *pubis*.

The hairs are very elastic; according to Weber, they stretch without breaking to nearly a third more than their length, and if they be stretched only a fifth, they contract again so perfectly, that they remain permanently only $\frac{1}{17}$th longer. They readily imbibe water, and as readily give it out again; they are therefore sometimes dry and brittle, sometimes moist and soft, according as the skin or the atmosphere contains much or little moisture. They become longer or shorter, according to the amount of moisture which they contain, whence their use in Hygrometry. In spite of their extensibility, their strength is considerable, and hairs of the head will bear at least 6 ounces without breaking.

The chemical composition of the hairs is not yet sufficiently understood, but they are chiefly composed of a nitrogenous substance, soluble in alkalies with the evolution of ammonia, and insoluble in boiling acetic acid. Scherer and von Laer consider it to be a combination of protein with sulphur, and the latter supposes, in addition, the existence of a small quantity of a substance similar to gelatine, whilst Scherer regards a second nitrogenous matter which he found, to be a product of decomposition. Mulder considers the substance of the hairs to be a protein compound combined with sulphamid, of which he finds 10 per cent. Besides their nitrogenous constituents, the hairs, as even the earlier investigations showed, contain a considerable quantity of dark or clear fatty matter, which may be extracted by boiling in ether and alcohol. From horn and epidermis, the substance of the hair is distinguished, according to Mulder, especially by its insolubility in acetic acid and by the same test, from albumen and fibrin. The hairs withstand putrefaction better than any other part of the body, so that even mummy hairs are found to be quite unchanged; in water they are not dissolved, except in Papin's digester. Metallic oxides colour the hair just as they do the epidermis; thus, for example, they are blackened by the salts of silver and manganese, sulphurets of these metals being pro-

duced. Chlorine bleaches them. The ash amounts to about 1—2 per cent., and contains oxide of iron (more in dark hair); oxide of manganese; silica (traces); phosphate of magnesia and sulphate of alumina were found by Jahn in white hairs; and according to Laugin, copper occurs in the greenish hairs of those who work in copper and brass.

§ 56.

With regard to their more intimate structure, two substances may be distinguished in all hairs without exception, and in many there are three: 1, the *cortical substance,* or better, *fibrous substance,* which constitutes by far the most considerable portion of the hair and determines its form; 2, the *cuticle,* a delicate external investment of the fibrous substance; 3, lastly, the *central medullary* substance, which is often absent.

The *cortical* or *fibrous substance* is longitudinally striated, very often presents dark dots, is streaked or spotted and except in white hairs, in which it is transparent, is more or less deeply coloured; the colour is sometimes distributed through the whole substance with tolerable regularity, sometimes more concentrated in certain elongated, granular spots. The more intimate structure of the cortex of the hair, and the signification of its spots and striæ, cannot be properly understood without the use of acids and alkalies (which afford important aid in the investigation of the hairs in general) and other manipulations. If a hair be treated with concentrated sulphuric acid at a warm temperature, its fibrous substance is much more readily broken up than before, into flat elongated fibres of various breadths (commonly 0·002—0·005‴), which are characterised particularly by their rigidity and brittleness, and by their irregular, even notched, margins and ends: in pale hairs they are clear, and in dark ones have a dark tinge. These so-called hair-fibres are not, however, the ultimate elements of the fibrous substance; each of them, in fact, consisting of an aggregation of flat, moderately-long fibre-cells or plates, which may be found isolated among the fibres after the thorough action of sulphuric acid. These (fig. 64), which may best be named the *plates of the fibrous substance,* or the *fibre cells of the cortex,* are flat and generally fusiform, 0·024—0·033‴ long, 0·002—0·004‴, or even 0·005‴ broad, 0·0012—0·0016‴ thick, with uneven surfaces and

irregular edges; they do not swell up into vesicles on the addition of caustic alkalies, and they very frequently exhibit a darker streak in their interior, of which we shall speak immediately; under certain circumstances they also contain granular pigment; for the rest they are homogeneous, and present no minuter elements, such as fibrillæ or the like. They appear to be more strongly united longitudinally, than in the direction of their breadth, whence it arises that the cortical substance easily breaks up into the long fibres above mentioned. The fibres themselves (which I should not be inclined to consider as compound elements of the cortical substance, since their constituents are separable, and they themselves are far too irregular), without constituting distinct lamellæ, like the plates of the nail and of the epidermis, form a compact fibrous bundle, and in this manner the cortical substance, which constitutes the principal bulk of the hair, is produced.

Fig. 64.

The *dark spots, dots,* and *streaks* of the cortex, are very various in their nature, and are principally: 1, *granular pigment;* 2, *cavities filled with air or fluid;* and 3, *nuclei.* The action of caustic potass and soda, which soften and swell up the cortical substance without attacking the spots (fig. 67), shows that they are in great measure nothing but aggregations of pigment

Fig. 64. Plates or fibre-cells of the cortical substance of a hair treated with acetic acid, × 350: *A*, isolated plates, 1, from the surface (3 single, 2 united); 2, from the side. *B*, a lamella composed of many such plates.

granules, which are deposited in the plates of the hair, are especially frequent in dark hairs, and vary very much in respect to their size and form. Dark spots of a second kind are very similar to the pigment deposits, but turn out on examination *to be little cavities filled with air*. They are best studied in white hairs, where they cannot possibly be confounded with pigment. Here we see dispersed through the whole cortical substance round dots of 0·0004—·0008''', or longish streaks of 0·004''' in length, 0·0004—0·0008''' in breadth, which, sometimes more scattered, sometimes more numerous and arranged in irregular lines, run parallel with the axis of the hair. The dark contours and somewhat clear centre of these, attract attention at once, and call to mind fat granules, which, in fact, for a long time I held them to be; but they are nothing but excessively minute cavities filled with air, which occur very frequently also in fair, bright-brown, and bright-red hairs, often in very great numbers, while they are wanting in very dark hairs, and in the lower half of the root of all hairs. Thirdly, there occur in the cortex, other tolerably dark striæ or lines, which in dark hairs are commonly connected with the pigment-spots, in such a manner that the striæ form the ends of the spots, or pass through them axially; in white and pale hairs they appear not unfrequently as prolongations of the air cavities, but in both kinds of hairs they often occur independently, in various numbers and degrees of distinctness. I hold these streaks, which are commonly most distinct in pale or bright-brown hairs without any medulla,

Fig. 65.

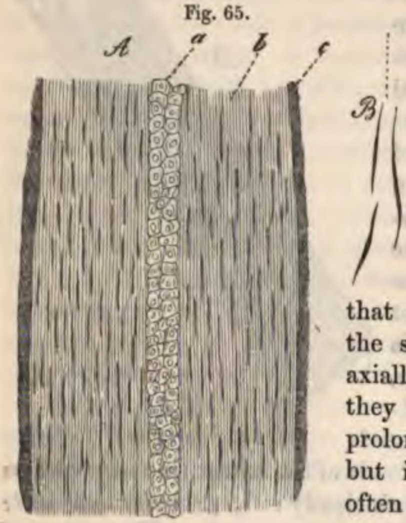


Fig. 65. *A*, a piece of a white hair after treatment with caustic soda, × 350: *a*, nucleated cells of the medulla without air; *b*, cortical substance with a fine fibrillation and prominent linear nuclei; *c*, epidermis with its plates projecting more than usual; *B*, three isolated linear nuclei from the cortex.

to be sometimes the expression of the composition of the hairs by the above-described fibre-cells; in other words, to be the boundary lines of the separate elements of the cortex, and sometimes I consider them to be their nuclei. For, even in the shaft of the hair, the cortical plates all contain fusiform nuclei 0·01—0·016‴ long, 0·0005‴—0·0012‴ broad, which may, in fact, be isolated by rubbing down white hairs which have been boiled in caustic soda. Besides these, there appear in the cortical substance, and with especial distinctness in a whitish place immediately above the bulb, certain fine striæ, which are produced by inequalities in the surface of the cortical plates and which do not readily disappear, even after the continued action of alkalies, but eventually give place to a finely fibrous appearance; they cannot be isolated, but are visible in those portions of the cortex which have been separated by sulphuric acid and sometimes even are very distinct (fig. 66).

The description of the *cortex*, which has just been given, holds good especially for the hair-shaft. In the root of the hair, so long as it is still solid and brittle, we find essentially the same conditions; and it is only in its lower half, where it becomes gradually softer, at first finely fibrous and then granular, that the structure of the cortex undergoes a progressive change. Here, in fact, the above-described plates are less rigid, and take on more and more distinctly the form of elongated cells (fig. 66) of 0·020—0·024‴ in length, and 0·009—0·011‴ in breadth, whose cylindrical, straight, or serpentine nuclei of 0·008—0·01‴, are very easily rendered visible by the action of acetic acid and may also be readily isolated. The soft and shortened plates then pass into elongated, rounded cells, with short nuclei, the fibrous structure becoming more and more obliterated, and these are finally continued without interruption into the elements of the lowest and thickest part of the hair, the bulb. They (fig. 67) are nothing more than round cells of 0·003—0·006‴, which lie closely pressed together; and like the cells

Fig. 66.

Fig. 66. Two cells from the cortex of the root of the hair (the finely-striated part of it immediately above the root), with distinct nuclei and a striated appearance, × 350.

of the mucous layer of the epidermis, sometimes contain only colourless granules, sometimes are so full of dark pigment-granules, that they become true pigment-cells. It must be added, that the chemical relations of the cortex are altered in the lower half of the root, its elements becoming more sensitive to the action of acetic acid, which does not affect the plates of the shaft at all; they swell up and dissolve in alkalies also, much more quickly than those of the shaft.[1]

Fig. 67.

The *colour* of the cortical substance arises partly from spots of pigment, to some extent from air cavities, and partly from a colouring matter diffused through and combined with the substance of the cortical plates. The first or the granular pigment, exhibits all shades from clear yellow, through red and brown, to black; the diffused pigment is quite absent in white hairs, and is scanty in clear, fair hairs; it is most abundant in the more opaque fair hairs and in red as well as in dark hairs, in which it may by itself give rise to an intense red or brown colour. The colour of the cortex depends especially upon that of these two pigments, but sometimes the one, sometimes the other predominates, and it is only in the very light and in the very dark hairs that they are developed in about equal proportions.

§ 57.

The *medullary substance* is a streak or cord which extends in the axis of the hair, from the neighbourhood of the bulb nearly to the point (figs. 65, 68). It is generally absent in the

Fig. 67. Cells from the deepest part of the bulb of the hair, × 350: *a*, from a coloured bulb, with pigment granules and somewhat hidden nucleus; *b*, from a white hair, with a distinct nucleus and but few granules.

[1] [Reichert ('Bericht' for 1850, Müll. 'Archiv,' 1851) asserts that the cortical substance of the hair is composed of superimposed laminæ, and recommends, in order to demonstrate the fact, that a hair should be treated with a solution of caustic potass of 10 per cent., and then submitted to pressure. Under these circumstances, "beautiful lamellæ appear. The separate layers exhibit no trace of being composed of fusiform cells; they appear finely striated, and in places, hyaline; sometimes elongated spots appear, of which it cannot be determined with certainty whether they are nuclei or perforations in the membrane." In some, there was no trace of these to be seen. Reichert considers the fibres of the cortex to be artificial products, and was unable to convince himself of the existence of nuclei in this part of the hair.—Eds.]

lanugo and coloured hairs of the head, but is usually present in the thick, short hairs, and in the stronger long ones, as well as in the white hairs of the head. If white hairs be boiled with caustic soda until they swell and coil up, we can often, by the use of simple pressure, demonstrate without further trouble, the cellular structure of the medullary cylinder, which is then transparent for transmitted light (fig. 65-*a*). If a hair thus treated be carefully teased out, it is easy to isolate the medullary cells, either in aggregate masses, or even completely separate (fig. 69). They are rectangular or quadrangular, rarely rounded or fusiform of 0·007—0·01‴ in diameter, occasionally containing dark, fat-like granules, and often when the alkali has not acted too strongly, a rounded clear spot of 0·0016—0·002‴, which is plainly the rudiment of a nucleus, and which also seems to swell up somewhat in soda.

Fig. 68.

Fig. 69.

In fresh hairs, the medulla in the shaft is silvery white or dark, an appearance which, as many more favorable objects show, arises from rounded-angular, granular corpuscles, black (opaque) or of a brilliant white, according to the illumination,

Fig. 68. A portion of the root of a dark hair slightly acted upon by caustic soda, × 250: *a*, *medulla*, still containing air, and with cells, which appear pretty distinct; *b*, cortex with pigment spots; *c*, inner layer of the epidermis; *d*, outer layer of it; *e*, inner layer of the inner root-sheath (*Huxley's* layer); *f*, outer fenestrated layer (*Henle's* layer).

Fig. 69. Eight medullary cells, with pale nuclei and fatty granules, from a hair treated with soda. × 350.

tolerably uniform in size, but varying according to the hairs, from 0·0002—0·002‴ and occupying the medullary cells in great quantity (fig. 68). These granules are not fat or pigment, as has been hitherto universally supposed, but *air-vesicles,* as may be readily demonstrated by boiling a white hair in ether or oil of turpentine, in both of which cases the medulla becomes quite clear and transparent. If such a hair, treated with water, be dried between the fingers, it soon, often quite suddenly and visibly to the naked eye, assumes its previous white colour, and if immediately after drying, it be placed under the microscope, without fluid, or with fluid at one end only, nothing is easier, than to see the re-entrance of the air and the consequent darkening of the medulla. Not only in white hairs, but in dark ones also, the medulla contains air in the fresh state, only in this case it does not appear of a pure silvery white, but with a blonde, red or brown tinge; this does not arise from any special pigment, which is only found occasionally in the medulla of dark hairs, but proceeds from its being seen through the coloured cortical substance. A more careful investigation of the medullary cells shows, that while fresh they contain many small cavities in a viscid substance; in these lie the air vesicles, which communicate to them the granular appearance above described. If we observe the air which has been expelled refilling the medulla of a dried hair, it seems as if all the cavities of one and the same cell communicated with one another, at least the air frequently passes in continuous winding streams from one cavity into the other; indeed from the sudden manner in which the air sometimes fills the medulla, it might almost be believed that the cavities of contiguous cells were connected together. However this may be in certain cases, it is conceivable, that even if the cavities of the different cells are quite closed, and only separated from one another by delicate partitions, the air still may quickly fill the medulla under the appearances we have noted. For the rest, the vacuities of the medullary cells, whether they are quite closed or not, are of different sizes, the aeriferous medulla appearing sometimes coarsely, sometimes finely granular. I have also seen cases in which the medullary cells obviously contained only a single, large air-vesicle, and appeared almost like small fat-cells. Very frequently single larger or smaller spots may be

observed in the medulla, which contain no air, and are thence pale and this is constantly the case in the lowermost part of the medulla, close above the bulb.

The medulla and the cortex are widely different if we compare the extreme forms of their elements; in the one case we have rigid homogeneous elongated plates, almost without contents, in the other rounded vesicles filled with fluid or air. If, however, we take into account all their conditions, we shall find that the limits are not so marked, and in fact are often hardly distinguishable. On the one hand, for instance, the medullary cells are not unfrequently of an elongated or short fusiform figure, whilst on the other the plates of the cortex present a considerable cavity containing pigment. If such plates contain, instead of pigment or the smaller air vesicles, air in a larger cavity, as occurs sometimes though not frequently, it is still more difficult to distinguish the two kinds of elements from one another, and the more so if, as in red hairs, the medulla and cortex are in places, or for considerable distances, not distinctly defined from one another, the superficial cells of the medulla being scattered and passing quite gradually into the plates of the cortex, which lie very close together and contain much air. It is not intended to imply, by this, that the *medulla* and the *cortex* are identical, but only that transitions exist, and that the differences which occur are less marked than is commonly supposed.

The diameter of the *medulla* is generally, in proportion to that of the hair itself, as 1 : 3—5; relatively and absolutely, it is thickest in short thick hairs, thinnest in the down and hairs of the head. In a transverse section it presents a round or flattened figure, and the cells which comprise it are disposed in 1—5 or even more longitudinal series.

[The medullary substance, the cells in which were first accurately described by G. H. Meyer, varies most of all the constituents of the hair. In the down and the hairs of the head, it has been stated, by some, that it is wholly absent, which is to be corrected thus far, that it is certainly generally absent in the former, and frequently in the latter, perhaps more frequently, in certain individuals. In white hairs, even those of the head, of a tolerable length and thickness, I have

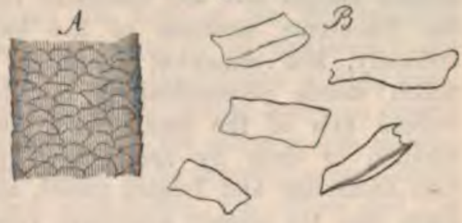
never failed to find it always beautifully distinct. In rare cases the medullary tract is double throughout (Bruns, figure in Hassall), more frequently divided in places into two tracts, which soon unite again. In the lower part of the root, the medulla, which is here clear, is often thicker, and exhibits the nuclei of its cells very distinctly, especially after the addition of acetic acid. Steinlin and Eylandt assert of the medullary substance, that it does not belong to the proper hair, but to its papilla, and originally represents a prolongation of this into the free part of the hair, which then dries up. This is incorrect. The *papilla* or germ of the hair is a part of the *cutis*, and has the same structure as the *papillæ* of the latter, whilst the *medulla* of the hair is composed of isolated cells, which by their resistance to alkalies, are in all respects allied to those of the epidermis. On the other hand, in animals, as has long been known, and as lately Bröcker has especially shown, the papilla often projects far, even to the point of the hairs, bristles or spines, subsequently drying up; but in these instances, according to Bröcker, it never, even after the action of potass, exhibits a cellular texture, whilst this is always obvious in the medullary substance, which is often present at the same time. Such an elongation of the papillæ may occasionally be noticed even in man, to a certain extent; thus Henle found it a few times prolonged into a short point. But any prolongation of this kind must be distinguished as decidedly from the cellular medullary substance, as in animals.]

§ 58.

The *cuticle of the Hair* (*cuticula*), is a very thin, transparent pellicle, which completely invests the hair, and is very closely united with the cortical substance. In its normal position, and observed in an unaltered hair, it is evidenced by hardly anything more than by numerous dark, reticulated, irregular or even jagged lines, which surround the hair at intervals of 0·002—0·006‴ from one another, and occasionally also by small serrations at its apparent edge (fig. 70 *A*); if, on the other hand, a hair be treated with alkalies, the cuticle is raised in smaller or larger lamellæ from the fibrous substance, and is even separated into its elements. These are quadrangular or rectangular flat plates without nuclei, generally pale and trans-

parent (fig. 70 *B*), which do not swell up into vesicles by the action of any reagent, and disposed in an imbricated manner, form a simple membrane which completely surrounds the *cortex* of the hair, in such a way, that the deeper or lower cells cover the upper ones. By sulphuric acid also, the structure of the epidermis is readily made out; the hair is, as it were, bristled at the edges with the erected plates and by scraping or rubbing, the cuticle is less easily obtained in large lamellæ, but is readily enough reduced to its elementary parts.

Fig. 70.



On the shaft of the hair the cuticle consists only of a single layer of plates 0·002—0·003‴ thick, which measure 0·024—0·028‴ in the transverse direction of the hair; 0·016—0·02‴ in that of its length; and are hardly more than 0·0005‴ in thickness. The same structure exists also in the upper part of the root of the hair; at its lower part, on the other hand, so far as the inner root sheath extends, two layers of the epidermis constantly occur. The outer (fig. 68 *d*) is rendered especially obvious by the action of soda or potass, and with a little pressure frequently comes away from the hair with the inner root sheath, whilst the inner layer becoming undulated, remains lying upon the cortical substance, and may be easily studied, as well in the side view as upon its surface. In hairs that are torn out, this layer is found only where they are covered by the inner root sheath, otherwise it remains behind in the hair-sac. Its elements also, are broad cells without nuclei, covering one another like tiles, which do not swell up in alkalies, and are soluble with great difficulty; they are thicker than those of the other layer, and measure only 0·002—0·004‴ in the direction of the length of the hair. The whole outer layer measures 0·0016—0·002‴, whilst the inner layer upon the root

Fig. 70. *A*, surface of the shaft of a white hair, × 160; the curved lines mark the free edges of the epidermic plates: *B*, epidermic plates from the surface, isolated by the action of caustic soda, × 350. One or both of their longer edges are bent round, and so appear dark.

has a thickness of 0·0025—0·0035‴. Upon the bulb of the hair, the two layers of cuticular plates pass with a tolerably defined margin into soft nucleated cells, which are broad in the transverse direction of the bulb, very short longitudinally, and somewhat longer in their third diameter, which stands perpendicularly or obliquely to the longitudinal axis of the hair. They are readily attacked by alkalies, or even by acetic acid, possess without exception transverse and longish nuclei, and finally pass, on the bulb, into the already described, round cells of which it is formed.[1]

[1] [We cannot agree with Prof. Kölliker that the cuticle of the hair passes into the outer cells of the bulb. It may be worth devoting a little space to this matter, as the whole question of the homology of the hair essentially turns upon it. So far from being able to trace the two layers of the cuticle into the round cells of the bulb, we find that they cease somewhat suddenly when the shaft begins to expand, while its substance is fibrous-looking and contains only much-elongated nuclei. Below this point, as Henle has correctly figured in his 'Allgemeine Anatomie,' Pl. I, fig. 14, the transverse striations of the cuticle are absent; and if the cuticular layer be viewed in section, it will be seen to be composed of a more transparent substance, which gradually becomes thinner until it is hardly distinguishable as a distinct layer, and at the same time loses the oblique lamination, which it has above, where it is continuous with the two layers of the cuticle proper. The careful addition of caustic ammonia is particularly fitted to demonstrate the structure of this part. In the first place, it raises up the outer layer of the cuticle from the inner, and shows that the former, at any rate, is not continuous with any cells; and secondly, it dissolves and forces out the substance of the lower soft portion of the bulb, so that the lower part of the cuticle may be obtained as a transparent, colourless, and independent sheath, even from the very darkest hairs; lastly, under favorable circumstances, this reagent raises up a definite basement membrane from the outer surface of the lowest part of the bulb, in immediate contact with the rounded "nuclei" of this part, and this basement membrane may be traced upwards into direct continuity with the homogeneous portion of the cuticle above-described. (In the 'Edinburgh Monthly Journal of Medical Science,' for March, 1853, Mr. Dalzell states that the papilla of the hair has a basement membrane. Is it this structure to which he refers?) In all cases in which, in man or in animals, we have isolated the hair-bulb from its sac, it seemed to have a definite limiting outer line down to the narrow neck by which it passes into the hair-sac, though it was not often easy to obtain evidence that this limiting line was the expression of a distinct basement membrane. However, the same difficulty would occur with any dermic papilla; and it seems to us that there is sufficient evidence to show that the cuticle of the hair is not the product of any direct metamorphosis of cells, but represents a modified basement membrane with a subjacent layer of peculiarly-altered blastema, corresponding precisely with the "Nasmyth's membrane" and the enamel of the teeth. *Vide infra*, § on Teeth.—Eds.]

§ 59.

The hair-sacs, *folliculi pilorum*, are flask-like follicles 1—3''' long, which embrace the roots of the hair tolerably closely, and, in the *lanugo*, are lodged in the substance of the upper layers of the corium, while in the stronger or long hairs, they generally project into its deeper portion, and even extend for a greater or less distance into the subcutaneous cellular tissue. These follicles are simply to be regarded as involutions of the skin, with its two constituents, the *corium* and the epidermis, and there may be distinguished, therefore, in each of them an external fibrous, vascular part, the proper hair-sac, and a non-vascular, cellular investment lining this,—the epidermis of the hair-sac; or, since it immediately surrounds the root of the hair,—the "root-sheath" (*vagina pili*).

§ 60.

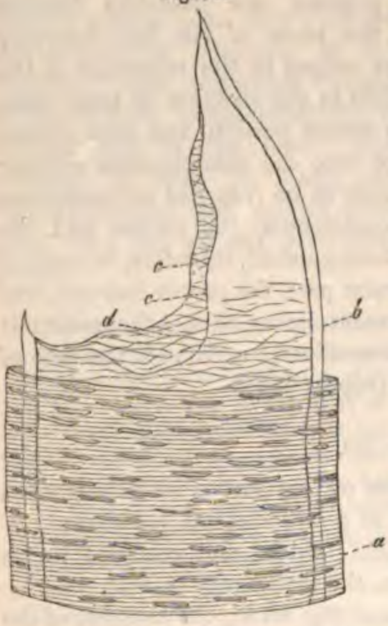
The *proper hair-sac* consists of two fibrous investments, an external and an internal, and of a structureless membrane; it is on an average 0·015—0·022''' thick, and contains in its lower part a peculiar structure, the *papilla of the hair*.

The *external fibrous membrane* (fig. 63 *h*), the thickest of the three layers of the hair-sac, determines its external form, and by its innermost layer is very closely connected with the corium. It consists of common connective tissue with longitudinal fibres, without any intermixture of elastic fibres, but with a considerable number of long fusiform nuclei; it contains a tolerably close plexus of capillaries, and exhibits also a few nervous fibrils with occasional divisions.

The *internal fibrous membrane* (fig. 71 *a*) is much more delicate than the external; bounded by smooth surfaces, and everywhere of equal thickness, it extends from the bottom of the hair-sac as far only as the entrance of the sebaceous glands. To all appearance, it contains neither vessels nor nerves, and is composed solely of a simple layer of transverse fibres, with long narrow nuclei, which may be seen particularly well in the empty hair-sacs of both coarse and fine hairs, with or without the addition of acetic acid. They resemble smooth muscular fibres, although they cannot be completely isolated and actually recognised as true fusiform fibres with a single nucleus;

on which account, and especially as no contractions of the hair-sacs have in general been observed, I must for the present refrain from positively deciding upon their nature.

Fig. 71.



The third layer, lastly (fig. 71 *b*), is a *transparent structureless membrane*, which, when the hairs are torn out, invariably remains behind in the hair-sac, and extends from its base, though, as it would seem, without covering the papilla, as far as the inner root-sheath, and perhaps higher. In the uninjured hair-sac it appears only as a pale streak 0·001—0·0015‴, rarely 0·002‴ thick between the outer root-sheath and the transversely fibrous layer of the hair-sac; by preparing an empty hair-sac, however, it can readily be obtained in large shreds, and then appears smooth externally; internally it is covered with very delicate, transverse, often anastomosing lines, which, like the membrane itself, remain unchanged in acids and alkalies. Neither acids nor alkalies bring out cells or nuclei in this membrane, and it therefore probably belongs to the category of true structureless membranes.

The *papilla of the hair* (fig. 63 *i*) also, less properly termed the hair-germ, *pulpa pili*, belongs to the sac, and corresponds with a papilla of the cutis. It is generally seen but indistinctly, especially in dark hairs with a coloured bulb, either appearing, only as a clear indistinctly-defined spot, or after the tearing out of the hair, remaining so covered by the cells of the bulb

Fig. 71. A piece of the transverse fibrous layer and of the structureless membrane (vitreous membrane) of a human hair-sac, treated with acetic acid, × 300: *a*, transversely fibrous layer with elongated transverse nuclei; *b*, vitreous membrane in apparent section; *c*, its edges, where the sheath which it forms is torn; *d*, fine transverse partly anastomosing lines (fibres) on their inner surface.

that nothing can be made out of it. It is only in the hair-sacs of white hairs that its outlines can be more frequently distinguished without wholly isolating it, especially by the help of a little pressure. Reagents, on the other hand, avail nothing, for they attack the *papilla* to about the same extent as the bulb, with the sole exception of a weak solution of caustic soda, in which it retains its outlines, for a time at any rate, whilst the cells of the bulb are freed and may be pressed out of the sac. The papilla is ovate or fungiform, $\frac{1}{8}$ — $\frac{1}{40}'''$ long, $\frac{1}{11}$ — $\frac{1}{20}'''$ broad, and is connected with the layer of connective tissue of the sac, by a pedicle: it has sharp contours and a perfectly smooth surface, and in its structure completely agrees with the papillæ of the *cutis*, consisting of an indistinctly fibrous connective tissue with scattered nuclei and fat-granules, but not of cells. I have taken every pains to discover vessels and nerves in the isolated *papillæ*, but in vain; even acetic acid and dilute solution of caustic soda, which in general do such excellent service in these cases, have failed, and Hassall and Günther met with the same results. It must not hence be concluded, that the *papilla* contains no vessels or nerves, for we know that in other places, where vessels do certainly exist, they often completely escape the eye; as, for example, in the dermal *papillæ* and in the *villi*; and with respect to the nerves, in the papillæ of the cutis. In some animals the vessels may very readily be seen.

§ 61.

The *root sheath*, or the epidermic investment of the hair-sac, is continuous with the epidermis around the aperture of the follicle, and may be divided into an external and an internal layer, which are distinctly defined from one another.

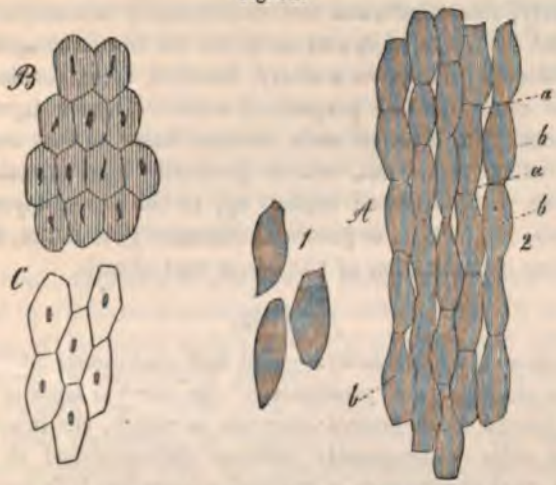
The *external root-sheath* is the continuation of the *stratum Malpighii* of the epidermis, and lines the whole hair-sac, resting for its lower half on the transparent membrane above described; higher up, when this and the transverse fibres are absent, it lies directly upon the longitudinally fibrous layer. Its structure corresponds exactly with that of the *stratum Malpighii*, even in the having the outermost cells, which in the Negro, according to Krause, are always brown, and in whites are so, at least in the hairs of the *labia majora*, towards the

upper part, arranged perpendicularly. At the bottom of the hair-sac, the outer root-sheath, its cells becoming gradually rounded, passes continuously, and without any sharp line of demarcation, into the round cells of the hair-bulb which cover the *papilla*. The outer root-sheath is generally about 3—5 times as thick as the inner; but not unfrequently it becomes thinned towards its upper part, and below invariably passes into a very thin lamella. In the coarse hairs it measures in the middle of the root 0·018—0·03‴, and presents 5—12 layers of cells.

The *inner root-sheath* (fig. 68—*e. g.*) is a transparent membrane which extends from almost the very bottom of the hair-sac, over more than two thirds of it, and then suddenly ceases. It is closely connected externally with the outer root-sheath, internally with the cuticle of the hair (its outer layer), so that normally there is no space between it and the hair; further it is distinguished by its great density and elasticity, and it consists in all but its lowermost part, of two or even three layers of polygonal, elongated, transparent, and somewhat yellowish cells, all of which have their longitudinal axes parallel to that of the hair (fig. 68). The outermost layer (fig. 72, *A*), which alone was formerly known, the inner root-sheath of Henle, is formed of elongated cells without nuclei, 0·016—0·02‴ in length, and 0·004—0·006‴ in breadth, which are intimately connected, and in the ordinary mode of investigation, after the addition of acetic acid, caustic soda or potass, which swell up the hair, or after the hair has been teased out, present elongated fissures between them, whence they appear like a fenestrated membrane. In quite recent hairs, however, if all reagents and mechanical injury have been avoided, we see hardly any trace of apertures in the *upper* half of the layer in question, and in the *lower* half (from the finely fibrous part of the cortex upwards), at most mere indications of them, in the form of striæ, clear or dark, according as they are in or out of focus, and similar to those of the cortex of the shaft. We can hardly avoid supposing, therefore, that the openings as they are commonly seen (0·005—0·008‴ in length, and 0·001—003‴ in breadth), are produced artificially by the teasing out of the membrane. Secondly, cells also occur in the root-sheath, between which gaps are never visible. These (fig. 72, *B*)

which form a simple or a double layer (*Huxley's* layer) are constantly situated internal to the common, and as far as I

Fig. 72.



have seen, always single, fenestrated layer of cells; they are shorter and broader than the cells which have already been described (0·014 to 0·018‴ long, 0·006 to 0·009‴ broad), but are also polygonal, and always possess, at least in the lower half of the root-sheath, distinct elongated nuclei often prolonged into points of 0·004—0·006‴. The diameter of the whole inner root-sheath is, upon the average, 0·006—0·015‴, whence it follows, that its cells, of which there are never more than three layers, are at least 0·002—0·005‴ thick. They are recognisable at once in their natural position, and by the teasing out of the root-sheath, and are readily isolated by the use of soda and potass (fig. 72), but without swelling up, a character which no less than their great resistance to alkalies altogether, distinguishes their cells, in common with the epidermic scales of the hairs, from all others.

At the bottom of the hair-sac the inner root-sheath consists only of a single layer of beautiful, large, polygonal, nucleated

Fig. 72. Elements of the inner root-sheath, × 350: *A*, from the outer layer, 1, its isolated plates; 2, the same in connection, from the uppermost parts of the layer in question, after treatment with caustic soda: *a*, apertures between the cells, *b*: *B*, cells of the inner not-perforated layer, with elongated and slightly notched nuclei; *C*, nucleated cells of the lowest part (single layer) of the inner sheath.

cells, without any intermediate openings (fig. 72, *C*), which becoming at last soft, delicate, and rounded, pass without defined limits into the outer layers of the round cells of the hair bulb. Superiorly, this membrane not unfrequently becomes somewhat separated from the hair, and ends, not far from the apertures of the sebaceous glands in a sharp, notched edge, formed by its separate more or less projecting cells. Thence upwards, it is replaced by a layer of cells, in some cases at first nucleated, but at other times not, which gradually approximates more and more, as it is traced higher up, to the horny layer of the *epidermis*, into which it passes continuously; it is not, however, any direct continuation of the inner root-sheath.

§ 62.

Development of the hairs.—The first rudiments of the hairs are flask-shaped, solid processes *of the mucous layer of the epidermis formed by its growth inwards*, in which, the internal and external cells subsequently become differentiated in such a manner, that the former, a gradual conversion into horn going on, are, in the axis of the rudiment, metamorphosed, in the first place into a small delicate hair, and secondly, around this into its internal sheath; while the latter, undergoing less alteration and remaining soft, constitute the outer root-sheath and the soft cells of the hair-bulb. Hence the hairs and their sheaths arise at once in their totality. The former, as minute hairs with root, shaft, and point, and are therefore not developed point first, as the teeth are, with their crown first, and still less as Simon has supposed, from their root first. The elements of the youngest hairs are nothing but elongated cells similar to those of the *cortex* of the later hairs, which are developed by the lengthening and chemical alteration of the innermost cells of the rudiments of the hairs. Medullary cells are entirely wanting, but the cuticle is clearly visible. The inner sheath is striated, presents no openings, and consists of elongated cells, which have been developed from those lying between the hair and the outer sheath. The proper hair-sac is formed, in its fibrous layers, essentially *in loco*, out of the formative cells which surround the rudiment of the hair; possibly, however, they may be considered as an involution of the *cutis*, produced by the ingrowing process of the epidermis. Its

structureless membrane, which appears very early, is, not improbably, closely related to the external cells of the rudiment of the hair, answering to the outer hair-sheath, and formed by an excretion from them like the *membranæ propriæ* of the glands; as to the *papilla* it is hardly possible to consider it as anything but an outgrowth of the fibrous layer of the hair-sac, analogous to the papillæ of the *cutis* in general; though the circumstance that it appears at a time when the hair-sac is hardly demonstrable as a whole, and that it may always be pulled out together with the rudiments of the hair and root-sheath, is apparently opposed to this view.

[The first rudiments of the downy hairs and of their sheaths, are found in the human embryo at the end of the third or at the beginning of the fourth month, upon the forehead and eyebrows. They consist of papilliform masses of cells 0·02‴ in diameter (fig. 73), which are visible, even to the naked eye, as minute whitish spots separated by regular intervals. They are continuously connected with the *rete Malpighii* of the *epidermis* and are nothing more than perfectly solid processes of it, which penetrate obliquely into the *corium*, and here lie in the meshes of a delicate capillary network; these cells are spherical 0·003—0·004‴ in diameter, and consist of a clear granular substance and round nuclei of 0·002—0·003‴. Nothing was to be seen of any dermic investment of these rudiments; in other words the foundation of what I have described as the proper hair-sac was not laid. In the fifteenth week the processes were already larger (0·025—0·03‴ long, 0·013—0·02‴ broad), flask-shaped, and surrounded by a thin structureless investment, which was continued into a delicate membrane lying between the cutis and the *rete Malpighii*, but united more closely with the latter. Besides this investment, which is, probably, only the structureless

Fig. 73.

Fig. 73. Rudiment of the hair from the brow of a human embryo, sixteen weeks old, × 350: *a*, horny layer of the epidermis; *b*, its mucous layer; *i*, structureless membrane surrounding the rudiment of the hair and continued between the mucous layer and the corium; *m*, roundish, partly elongated cells, which especially compose the rudiment of the hair.

membrane which I have discovered in the perfect hair (see § 60), another, external layer of cells occurs on the hair-sacs, which can generally be separated only in shreds with it, from the *cutis*, rarely altogether: this I regard as the first indication of the fibrous layers of the hair-sacs. In the 16th and 17th weeks the processes of the mucous layer, which I will henceforward simply call "hair-rudiments," increase in size up to ·004—0·06‴ length, and 0·03—0·04‴ breadth, and acquire thicker coverings, but as yet exhibit no trace of a hair. In the 18th week these first appear in the eyebrows, as hair-rudiments of 0·1—0·2‴, their central cells becoming somewhat elongated, and arranging themselves with their longitudinal axes parallel to that of the rudiment, whilst the peripheral cells are disposed with their now longer diameter transversely. A variety of shade in the hitherto homogeneous hair-rudiment arises in this manner, and a central substance, broad below, running above into a sharp point, becomes marked off from an outer portion, which is narrow below and thick above. When the rudiment has attained a length of 0·22‴, this marking off is still more distinct, the rather longer and especially broader, inner cone having a somewhat clearer appearance (fig. 74). Finally, in rudiments of hair of 0·28‴, the inner cone is divided into two structures, a central portion somewhat darker, and an external, perfectly transparent and glassy,—the hair and the inner root-sheath,—whilst the peripheral cells which have remained opaque, constitute unmistakeably the outer root-sheath (fig. 75 *A*). At the same time the *papilla*, which was even before (fig. 74) just traceable, becomes more distinct, and the proper hair-sac also more recognisable, as the cells which lie external to its structureless membrane begin to pass into fibres which may, even at this time, be known by their decussation. The hair-sacs and hairs arise, in other places exactly in the same manner as in the eyebrows, except that their development takes place somewhat later. In the 15th week, no rudiments of hairs are visible, except on the forehead and eyebrows; in the 16th and 17th week they appear all over the head, back, chest, and abdomen; and not till the 20th week on the extremities. The hairs themselves never make their appearance earlier than 3—5 weeks after that of the rudiments; in the 19th week, for example, the commencement of hairs is nowhere to be seen, except on the forehead and

eyebrows; and in the 24th week they are still absent upon the hand and foot, and partly on the fore-arm and leg.

Once formed, the hairs and hair-sacs continue to grow. The former sometimes penetrate the epidermis immediately

Fig. 75.

Fig. 74.

(eyebrows, eyelashes, fig. 75), sometimes their points are insinuated between the horny layer and the *stratum Malpighii*, or among the elements of the horny layer itself, and grow for a time covered by the *epidermis* (chest, abdomen, back, extremities [?]), through which they eventually make their passage. Involutions of the skin growing towards the hairs as they pass out, never exist, and the supposition that they do, rests upon a wholly subjective foundation.

Fig. 74. Rudiment of a hair from the eyebrow (0·22‴ in length), × 50, its inner cells forming a distinct cone, as yet without any hair, but with the papilla indicated: *a*, horny layer of the epidermis; *b*, mucous layer; *c*, outer root-sheath of the subsequent sac; *i*, structureless membrane upon its outer side; *h*, papilla of the hair.

Fig. 75. *A*, rudimental hair from the eyebrows, with just developed but not yet erupted hair, of 0·28‴ in length. The inner root-sheath projects beyond the point of the hair somewhat at the upper part, and laterally at the neck of the sac; the first rudiments of the sebaceous glands appear in the form of two papillary outgrowths from the outer root-sheath. *B*, hair-sac from the same, with its hair just erupted; the inner root-sheath projects through the aperture of the hair-sac; the rudiments of sebaceous glands are as yet not developed; the letters *a*, *b*, *c*, *h*, *i*, have the same signification as in fig. 74: *e*, hair-bulb; *f*, hair-shaft; *g*, hair-point; *n*, rudiments of the sebaceous glands.

The downy hairs, *lanugo*, the eruption of which is completed in the 23d—25th week, are short fine hairs, whose peculiar arrangement has been noted above. They measure on the bulb 0·01‴, on the shaft 0·006‴, at the point 0·0012—0·002‴; are pale, or almost colourless, and consist only of cortical substance and a cuticle. In man, the bulb is usually colourless, and often rests upon a very distinct *papilla*, arising in the ordinary manner from the bottom of the hair-sac. It has the same three layers as in the adult, and possesses a very well-developed epidermic investment, consisting of an external root-sheath of 0·004—0·012‴, and an inner sheath of 0·006—0·008‴, without openings.

After their eruption, the downy hairs grow slowly to a length of $\frac{1}{4}$—$\frac{1}{3}$ of a line, and in fact to a greater length in the head than elsewhere. Generally they remain to the end of fœtal life, gradually acquiring a darker colour, becoming in many cases, as on the head, even blackish; another small portion falls off into the *liquor amnii*, is swallowed with this by the fœtus, and may afterwards be found in the meconium. A proper shedding of the hair does not take place at all in the fœtus, so far as I can see, infants being born with the *lanugo;* as little does any trace of a further formation of hair appear after its complete eruption.

The question whether the point of the hair is first formed, or whether the latter is developed at once as a whole, is readily solved. Hairs which are just formed, have a bulb with soft cells, a horny point and an intermediate portion, in which the cells are converted into horn, and are partly found passing into the cells of the root, whence there can be no doubt that we have here a whole hair. That the horny part of this hair subsequently forms the point of a larger hair, is of no importance; and as little as the hairs of the head of a newly-born infant can be called points of hairs, because they subsequently become the points of larger hairs, can we so denominate these. Nor can it be said that the first fœtal hair subsequently becomes, in totality, the point of a larger hair, since the hairs do not grow by the simple apposition of new elements, like the bones, but by the multiplication of their lowest soft cells, some of which are always retained as a reserve for cells to be newly developed, whilst the others are converted into horn; whence

also it happens, that the cells even of a complete hair-bulb are to be regarded as the successors of those of the fœtal hair.][1]

§ 63.

Shedding of the Hair.—After birth, a total shedding of the hairs takes place in consequence of the development of new hairs within the hair-sacs of the lanugo, which gradually force out the old ones. This shedding of the hairs, which I discovered in the eyelashes of a child of one year old, commences by an outgrowth of the soft round cells of the bulb and of the neighbouring outer root-sheath, from the bottoms of the sacs of the

[1] [From what has been said above (see note on the Cuticle) it is clear we do not share Professor Kölliker's view that the hair is an epidermic production. Reichert's view, on the other hand, that the hair results from the cornification of a dermic papilla or matrix, which drying up and becoming filled with air, remains as the medullary portion, seems to us to be nearer the truth. There can be no doubt of these two facts: 1, that no line of demarcation can be traced between the papilla of the hair and its shaft; and 2, that in many animals the papilla is vascular and nervous for a considerable distance into the shaft, and, therefore, is certainly a dermic structure.

Whether Reichert's somewhat mechanical notion of the "drying up" of the matrix to form the medulla is correct, is not of much importance, so long as we keep in view the unquestionable continuity of tissue and homological identity, of the medulla and cortex with the dermic papilla.

For us, in fact, the Hair is homologous in all its parts with the Tooth. The substance of the shaft corresponds with the dentine, offering even rudimentary tubes in its aeriferous cavities; the inner layer of the cuticle answers to the enamel, the outer to Nasmyth's membrane; and whoever will compare these structures will be struck by the similarity even in their appearance. The sac answers to the dental capsule; the outer root-sheath to the layer of epithelium (enamel organ) next the capsule; the fenestrated membrane to the stellate tissue; and what Professor Kölliker calls "Huxley's layer," to the columnar epithelial layer of the *organon adamantinæ*. The comparison may seem startling at first, but the examination of the development of the teeth of an osseous fish, for example, will suffice, we believe, to afford full justification of it.

With respect to the not very important question, as to the nature of the first rudiment of the hair-shaft, *i. e.* whether it is the point of a hair or a whole hair, we must confess that we should be tempted to arrive at the opposite conclusion to our author. Inasmuch as the portion of the hair which first appears becomes the point of the fully-grown hair, we should say that the hairs *are* formed like the teeth, point first.

A hair, like a tooth, has a definite form to attain. As the latter has a peculiarly constructed and narrowed root when complete, so has the hair when it has attained its full growth a peculiarly constructed bulb; and it is not a perfect hair until this peculiar bulb is developed. Until it has attained this form it goes on growing; but once having reached it, it grows no more, but falls out and is replaced by a new hair (see following §).—Eds.]

lanugo, into long processes composed of cells, by which the hair is raised from its papilla, whilst at the same time it becomes converted into horn even in its lowermost portion. When these processes have attained a length of 0·25‴, a differentiation of their outer and inner cells takes place, similar to that which has been already described as occurring in those processes of the *stratum Malpighii*, in which the hairs of the *lanugo* are developed. The outer cells, in fact, remaining round and colourless, as they were before, the inner ones begin to develope pigment in their interior and to elongate, becoming distinguished at the same time from the former, as a conical substance with its point directed upwards. At first (fig. 76 *A*), this central substance is quite soft, and like the layers of cells which surround it externally, dissolves readily in solution of caustic soda; subsequently, however, when, together with the process which incloses it, it has elongated, its elements harden, and separate into two portions, an internal dark pigmented, and an external clear part, which are nothing else than a young hair, together with its inner sheath (fig. 76 *B*). The young hair, whose point at first does not project beyond its inner root-sheath, now grows gradually, forcing its point through the aperture of the old sac, while at the same time its root-sheath elongates, and thrusts upwards the bulb of the old hair, until

Fig. 76.

Fig. 76. The eyelashes of a child of one year old pulled out, × 20: *A*, one with a process of the bulb or of the outer root-sheath, of 0·25‴, in which the central cells are elongated (their pigment is not represented), and are clearly defined as a cone from the external ones; *B*, eyelash in whose process, of 0·3‴, the inner cone is metamorphosed into a hair and an inner root-sheath; the old hair is pushed up, and like *A* and fig. 75, possesses no inner root-sheath: *a*, outer; *b*, inner root-sheath of the young hair; *c*, pit for the papilla of the hair; *d*, bulb; *e*, the shaft of the old hair; *f*, bulb; *g*, shaft; *h*, point of the young hair; *i*, sebaceous glands; *k*, three sudoriparous canals, which in *A* open into the upper part of the hair-sac; *l*, transition of the outer root-sheath into the *rete mucosum* of the epidermis.

at last it passes completely out, and makes its appearance at the same opening with the old one, which is more and more pushed up. When the development of the hair has gone thus far, the last stage may be readily understood. The old hair, which has for a long time ceased to grow, and to be connected with the bottom of the sac, being thus extruded, falls out, while the young hair becomes larger and stronger, and fills the gap left by the old one. The primary cause of the dying away and casting off of the old hair, I consider to be the development of the processes of the hair bulb and outer sheath from the bottom of the sac, which has been described. As the sacs do not elongate to a corresponding extent, they push upwards all those parts which lie above them, and cause a continually increasing space to exist between the papilla and the proper hair, or the point at which the round cells of the bulb begin to elongate and undergo conversion into horny matter.

Fig. 77.

The hair thus becomes in a manner detached from the source of its nourishment; it receives less and less blastema, at last ceasing to grow, and becoming converted into horn in its lowest part. The cells of the processes, on the other hand, which are connected with the papilla, are incessantly supplied from it with new formative material, which for the time they apply not to the formation of horny matter, but to their own growth. In this manner the processes continue to grow, and mechanically elevate the cornified root of the old hair, with its sheaths, to the aperture of the sebaceous glands, where to all appearance a partial solution of the old sheaths takes place: this may be observed with certainty in the inner sheath, and must be assumed to occur in the outer.

All that has been said, holds good only with respect to the

Fig. 77. An eyelash with the root-sheaths from a child one year old, with an old and a growing young hair, × 20; the young hair is wholly extruded, and now two hairs appear at one aperture. A sudoriparous canal opens into the hair-sac. The letters have the same signification as in fig. 76.

eyelashes. The hairs of the head, and the other hairs of the body of the child (almost a year old) in question, never contained more than one hair, though their bulbs presented processes without hairs like those which precede the shedding of the eyelashes; such processes, in fact, being of *very common occurrence* in the hairs of children within the first year. I believe I am not wrong, if from the presence of these processes I deduce the universal occurrence of a shedding of the hairs, particularly as it is certain that in many children within the first 2—6 months after birth, the hairs of the head fall out and are replaced by new ones. However, further observation is necessary to determine what period is occupied by this first shedding of the hair, in what hairs it occurs, and whether perhaps the process is subsequently repeated.

[If we compare the shedding of the hairs with their first development, we find a great resemblance between the two processes. In both, elongated projections, wholly formed of round soft cells, shoot like buds from the *stratum Malpighii*, in the one case of the skin itself, in the other of the hair-sacs and hairs. In both, a separation of the inner from the outer cells next takes place; and while the latter are metamorphosed into the outer root-sheath, the former become the inner root-sheath and the hair. The latter arises, as is still more clear in the shedding of the hairs than in their first development, like the nail, with all its parts at once, as a small hair provided with point, shaft, and root, and which only subsequently begins to grow, in consequence of which it enlarges in all its parts, and finally reaches the surface. The differences between the two modes of development are very inconsiderable, and chiefly depend upon the rudimentary hair-processes, in the one case proceeding from the hairs themselves, but not in the other; and upon the circumstance that the young hairs, although in both cases they lie at first in a closed space, reach the surface more readily in the one case, than in the other.

In the periodical shedding of the hair of animals, the observations of Heusinger and Kohlrausch, and lately those of Langer, Gegenbaur and Steinlin, show that the new hairs are also developed in the sacs of the old ones; although, according to the last author, with whom however Langer is not quite in

accord, the process does not appear to be exactly the same as in man.

§ 64.

Physiological Observations.—The hairs have a definite length, dependent upon locality and sex, but if they are cut they grow again, and consequently exhibit the same conditions as the other horny textures. The place from whence the growth of the hair proceeds is unquestionably the bottom of the hair-sac. Here there arise around the papillæ, with the co-operation of a blastema formed out of its vessels or those of the hair-sac, new elements, by the continual multiplication of the existing cells, while those which are already present, somewhat higher up pass uninteruptedly, the middle ones into medullary cells, the next into cortical plates, the outermost into epidermic scales, and thus the horny part of the hair is continually forced from below upwards, and elongates. In the latter no formation of elementary parts takes place, but at most a certain metamorphosis of those which are already existent, which produces a gradual thinning of the root from the bulb upwards, until it acquires the thickness of the shaft. Higher up still, these changes of the elementary parts cease, whence cut hairs, for example, do not produce new points. The root-sheaths and the outer layer of the epidermis take no part in the growth of cut hairs.

The complete hair, though non-vascular, is not a dead substance. Although the processes which go on in it are not at all understood, we may suppose that fluids are diffused through it which subserve its nutrition and maintenance. These fluids are furnished from the vessels of the papilla and sac of the hair, in all probability ascend (particularly from the bulb) without any special canals through the cortex upwards, and thus reach all parts of the hair. Having served for the nutrition of the hair, they evaporate from its outer surface and are replaced by a fresh supply. Perhaps the hairs also absorb fluids from without, though of course only in the condition of vapour, like a hair used as a hygrometer; on the other hand I cannot believe that, as many authors would seem to suppose, the secretion of the sebaceous glands passes from without into the hairs, since the perfectly closed cuticle is probably impervious to it. In the same way it seems to be in

nowise proved that the hairs are pervaded by a peculiar oleaginous fluid (Laer), which might proceed from the medullary substance (Reichert), and which keeps it greasy, for such a fluid has not been demonstrated, and the greasiness of the hairs may be more simply explained by the externally adherent sebaceous matter, which is readily visible. The existence of air in the medullary axis and in the cortex can only arise from a disproportion between the supply of fluid from the hair-sac and the amount evaporated; it is owing, as it were, to a drying-up of the hair, which, however, must not be supposed to go so far that the hair contains no fluid in its aeriferous portion. In any case, however, these portions are the most inactive, or relatively dead parts of the hair; the cortex, on the other hand, which is also most readily altered by alkalies and acids, notwithstanding the apparent hardness and density of its elements, is the most rich in juices, and is that in which the nutritive process is most actively going on. Hence it follows, that the hair lives, and is to a certain extent dependent upon the collective organism, particularly on the skin, from whose vessels (*i. e.* those of the hair-sac) it derives the materials necessary for its maintenance. Therefore, as Henle well says, the condition of the hair is a sort of index of that of the activity of the skin; if they are soft and shining, the skin is turgescent and transpires; if they are dry, brittle, and rough, then it may be concluded that the surface of the body is in a collapsed condition.

The falling out of the hairs certainly depends, in many cases, —when, for example, it takes place in the course of normal development,—on nothing else than a want of the necessary nutritive material, which in the instance already explained, in speaking of the shedding of the hairs, depends on the detachment of the hair from its matrix by the abundant production of cells at the bottom of the hair-sac. In age, perhaps, it arises simply from the obliteration of the vessels of the hair-sacs.

The whitening of the hairs, which chiefly depends upon a decoloration of the cortex, and less upon that of the almost colourless medulla, should probably be here considered, for its normal occurrence in old age gives it the significance of a retrogressive development.

The frequent occurrence of cases, in which the hair grows

grey first at its point or in the middle, and the well-established instances of its rapidly becoming white, are interesting, and strongly testify to the vitality of the hair; but it has not yet been shown, what peculiar processes in the elements of the hair produce the decoloration of its different pigments.

As in youth hairs which are shed are replaced by others, so at a later age something similar appears to occur. It is quite certain that during the period of full health and activity, a continual replacement of the numerous hairs which fall out goes on; furthermore that new hairs in great numbers spring up at the time of puberty in certain localities, but the manner in which this takes place is unknown. Inasmuch as even in adults we find hair-sacs with little processes downwards, whose proper hair has an abrupt clavate end, as in the child; since further, in this case it not unfrequently happens that two hairs come out of one aperture, and even exist together in one sac; and, finally, since in hairs which have fallen out spontaneously, we invariably find roots like those[1] which exist in the extruded hairs of the first shedding, it may be assumed that an actual shedding of the hairs occurs, even at a later period, in such a manner that the old hair-sacs produce new hairs while they throw off the old ones. I do not, however, intend to affirm by this, that an actual new formation of hairs does not occur after birth, but only this much, that in adults they are certainly regenerated from the already existing hair-sacs, especially if it be recollected that, according to Heusinger's observations, the whiskers of dogs, when pulled out, are reproduced from the same sacs in a few days, and also that during the shedding of the hair in adult animals, according to Kohlrausch, the young hairs are produced from the old sacs. Also, when the hairs which have fallen

[1] [Henle ('Allg. Anat.,' p. 303) gives a very excellent description of this state of the hair-bulb: "Instead of the soft cellular hair-bulb, we find an inconsiderable clavate enlargement, which is solid and fibrous, like the substance of the shaft, only more clear. From its outer surface, short and irregular processes project downwards, which are probably the notched lower edges of the outermost layers of the cortical substance; they look like fibres connecting the hair with the inner wall of the sac. This kind of root is found in hairs which have fallen out spontaneously, and it is, therefore, probable that it belongs to a later stage of development of the hair, or rather marks the conclusion of its development. When the connection with the sac has ceased, which is the case in these clavate roots, the hair grows no longer; probably it is no longer nourished, but falls out."—Eds.]

out after a severe illness, are replaced, it is more probable, since, according to E. H. Weber, the sacs of lost hairs remain for a long time, that they arise in the old sacs, than that new ones are developed.[1]

[The multiplication of the cells of the bulb of the hair during its growth takes place unquestionably, not by free cell-development, since no trace of anything of the kind is to be seen in any bulb, but either by endogenous cell-development round portions of contents, or by division. I do not think that all those hairs which possess a sharply-defined clavate bulb are on that account dead and ready to fall out. It is certainly thus in many cases; but in others this condition indicates nothing more than the normal termination of growth, whence of course, it does not follow that the nutrition also has ceased. In proof of the occurrence of a continual development of the hairs independently of the old hair-sacs, the hairs which lie spirally curled up under the epidermis and subsequently break through it, upon the forearm, leg, &c., are frequently cited. But I do not know that it would not be more correct to consider this, with many pathologists, rather as an abnormal process. In the first place this formation of the hairs by no means occurs in all persons; and secondly, where it does, there are found together with those coiled-up hairs, which are apparently normally developed, others which are evidently abnormal, in great quantities. These, often in considerable number (up to 9), with thick sheaths, lie in one sac and have rounded points, with irregular bulbs. With respect to their relations, it might for the present be wiser, so long as an actual, normal new development of hairs has not been demonstrated, not to assume it, and to consider that, even at a later period, the development of new hairs within the old sacs is the normal mode, especially since Dr. Langer has actually observed it to take place in many

[1] [Berthold (Müll. 'Archiv.,' 1850) has communicated some curious statistics relative to the growth of Hairs. The hairs of the head of a female of from 16 to 24 years of age, grow at the rate of 7 lines a month. The growth of the hairs of the beard is quicker the oftener they are cut; shaved every 12 hours, they would attain a length of from $5\frac{1}{2}$—12 inches per annum; every 24 hours, from 5—$7\frac{1}{2}$ inches; every 36 hours, from 4—$6\frac{1}{2}$ inches. They grow faster by $\frac{1}{18}$ during the day than during the night; and in 18 days of summer, 0·026 more than in 18 day of winter.—Eds.]

instances in the very same manner as that which I have described in children. The reason why the hairs grow continually, if they are cut, but not otherwise, is the same as I have already adduced, to account for the same occurrence in the nails. The vessels of the papilla excrete a certain quantity of nutritive fluid, just so much as is sufficient to keep the whole hair continually moist and in a state of vitality. If the hair be cut, more nutritive fluid is supplied than the hair can use, and therefore it grows by the aid of the superfluity until it has attained its typical length again, or if it be continually cut, it as continually grows.

Dzondi, Tieffenbach ('Nonnulla de regeneratione et transplantatione,' Herbip, 1822) and Wiesemann (De coalitu partium, Lips. 1824) have succeeded in transplanting the hairs with their sacs. Hairs are developed also in abnormal places, *e. g.* on mucous membranes, in encysted tumours, ovarian cysts, and in all these cases, even in the lungs (Mohr's case), possess sacs, root-sheaths, and an otherwise normal structure. No hairs are developed upon cicatrices of the skin. No satisfactory reason can be given for the excessive growth of the hairs, nor for their morbid universal falling out, together with their frequent reproduction in the same way; probably the principal causes are to be found in increased or diminished exudations from the vessels of the papilla and of the hair-sac, and more remotely in the state of the skin and the organism in general. In other cases vegetable productions (*fungi*) in the interior of the hair itself (in *Herpes tonsurans*, the "*Teigne tondante*," *Mahon*, according to Gruby ['Gaz. Méd.,' 1844, No. 14], and Malmsten, (Müll. 'Arch.,' 1848, 1), or under the epidermis of the hair and around it (in the *Porrigo decalvans* of Willan according to Gruby), are concerned in the production of baldness, which then is limited (*Alopecia circumscripta*). The process of becoming grey is also obscure, although grief, excessive intellectual activity, and nervous influences are sometimes evidently concerned in it. It is not until physiology and chemistry have approached these latter processes, that we can hope for a scientific pathology and treatment of the hair. *Plica polonica*, which, according to Bidder (l. c.), is a disease of the shaft of the hair, is said by Guensburg and Walther (Müller's 'Archiv.,' 1844, p. 411, and 1845, p. 34), to arise from a *fungus* which

is developed in the hairs (bulb, shaft), and partly destroys them; whilst Münter (ibid., 1845, p. 42) could find no such fungus. This disease, as well as peculiar yellowish-white rings upon the human hairs, consisting of epithelial cells without nuclei (Svitzer, in 'Fror. Notizen,' 1848, No. 101), which appear to consist of an altered secretion of the sebaceous glands, are less interesting from a histological point of view, and therefore are but shortly adverted to here.

For microscopic investigation, a white hair with its sac should be chosen in the first instance, subsequently coloured ones. Transverse sections may be obtained, either by shaving twice at short intervals (Henle), or by cutting hair on a glass (H. Meyer), or in a bundle between two cards (Bowman), or fixed in a cork (Harting); longitudinal sections, by slicing a finer or splitting a coarser hair. The hair-sacs may be examined, both isolated and with the hair; their different layers may be separated by preparations, and the nuclei of the external ones may be demonstrated by acetic acid. Concerning the *papillæ*, all that is necessary has been said above; the whole upper part of the root-sheath generally follows the hair when it is torn out, and in the macerated skin it comes out very readily with the hair; its cells may be made out without addition, or by a little acetic acid or caustic soda. The inner root-sheath is often to be found entire in torn out-hairs, and may without further preparation, or by stripping off the outer sheath, be readily recognised in all its parts. Caustic soda and potass acting for a short time, make it still more distinct. The *cuticle* must particularly be examined with alkalies and sulphuric acid, like the hair itself. The most important details upon this point have already been given, and more may be found in Donders (l. c.). I will only add that in this case also, the application of a high temperature (see above, in the section on the nails) saves much time. In investigating fœtal hairs, in the very young state it is sufficient to tear off the *epidermis*, attached to which the rudiments of the hairs will be found. In older embryos fine sections of the skin must be made; or the epidermis, and the corium may be stripped off together, in which case caustic soda is of assistance.

Literature.—Eble, 'Die Lehre von den Haaren in der gesammten organischen Natur.,' 2 Bde., Wien, 1831; Esch-

richt, 'Ueber die Richtung der Haare am menschlichen Körper,' in Müll. 'Arch.,' 1837, p. 37; V. Laer, 'De structurâ capill. hum. observationibus microscopicis illustr.,' 'Dissert. inaug.,' Traject. ad Rhenum, 1841, und 'Annelin der Chemie u. Pharmacie,' Bd. 45, No. 147; G. Simon, 'Zur Entwicklungsgeschichte der Haare,' Müll. 'Arch.,' 1841, p. 361; Krause, article 'Haut.,' in Wagners 'Handwörterbuch d. Phys.,' 1844, Bd. II, p. 124; Kohlrausch, 'Ueber innere Wurzelscheide und Epithelium des Haares,' Müll. 'Arch.,' 1846, p. 300; Jasche, 'De telis epithelialibus in genere et de iis vasorum in specie,' Dorpat, 1847; Kölliker, 'Ueber den Bau der Haarbälge und Haare,' in the 'Mittheil d. zürch., naturf.,' Ges., 1847, p. 177; Hessling, 'Vom Haare und seinen Scheiden in Froriep neue Notizen, 1848, No. 113; Langer, 'Ueber den Haarwechsel, bei Thieren und beim Menschen,' in den 'Denkschr. d. Wien,' Akad., 1850, Bd. I. The comparative anatomy of the hairs is treated of by Heusinger in Meckel's 'Arch.,' 1822, 1823, und 'System der Histiologie;' Erdl, in 'Abh. d. Münch.,' Akad., Bd. III, ii; Gegenbaur, in 'Verhund. d. phys. med. Gesellschaft zu Würzburg,' 1850; Steinlin, in 'Zeitschrift, für rationellen Medizin,' Bd. IX. The allied horny tissues are described in the 'Dorpat. dissertations,' by Bröcker, 'De texturâ et formatione spinarum,' 1849; Hehn, 'De text. et form. barbæ Balænæ,' 1849; Schrenk, 'De formatione pennæ,' 1849.

IV.—OF THE GLANDS OF THE SKIN.

A. OF THE SUDORIPAROUS GLANDS.

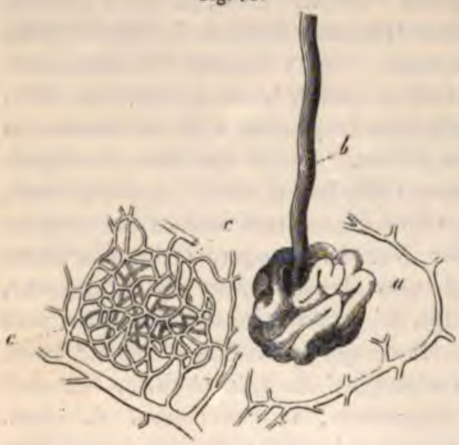
§ 65.

The *sudoriparous Glands* consist of a single delicate, more or less convoluted tube, which secretes the sweat. They are formed over the whole surface of the skin, with the exception of the concave side of the concha of the ear, of the external auditory meatus, the *glans penis*, one lamella of the prepuce, and a few other localities; and, open upon it by numerous fine apertures.

§ 66.

In every sudoriparous gland (fig. 45, fig. 78), we may distinguish, the *glandular coil* (fig. 78 *a*, fig. 75 *g*), or the *proper gland*, from the excretory duct or sudoriparous canal (fig. 45 *h*, fig. 78 *b*). The former is a rounded or elongated corpuscle of a yellowish or transparent yellowish-red colour, which in general measures $\frac{1}{7}$—$\frac{1}{5}'''$; but on the eyelids, the integument of the *penis*, *scrotum*, nose, convex side of the concha of the ear, on the other hand, not more than $\frac{1}{10}$—$\frac{1}{12}'''$; whilst on the areola of the nipple and in its neighbourhood, at the root of the penis, and between the scrotum and perinæum, it attains as much as $\frac{1}{2}'''$, and in the hairy parts of the axilla reaches as much as $\frac{1}{2}'''$—$1'''$—$1\frac{1}{2}'''$ in thickness, and 1—$3'''$ breadth.

Fig. 78.



The sudoriparous glands, in most cases, are lodged in the meshes of the *pars reticularis* of the corium, sometimes more superficially, sometimes deeper, surrounded by fat and loose connective tissue, together with or among hair-sacs. They occur more rarely in the subcutaneous connective tissue, or at its boundaries, as for example in the axilla, to some extent in the *areola mammæ*, in the eyelids, *penis*, and *scrotum*, the palm of the hand and sole of the foot. In the two last-named localities, they are disposed in rows under the ridges of the cutis, and at tolerably equal distances apart; in other places they are met with, usually in a regular manner, singly or in pairs, in each mesh of the *corium*, although, according to Krause, spaces of $\frac{1}{4}$—$\frac{1}{2}'''$ line exist, where they are totally absent, or

Fig. 78. A sudoriparous coil and its vessels, × 35 : *a*, glandular coil ; *b*, excretory duct or sweat duct ; *c*, vessels of a glandular coil, according to Todd and Bowman.

occur in groups of 3 or 4 close together. In the axilla, the glands form a *connected layer* under the corium.

According to Krause, there occur on a square inch of the skin between 400 and 600 glands on the back of the trunk, the cheeks, and the two superior segments of the lower extremities; 924—1090 on the anterior part of the trunk, on the neck, brow, the fore-arm, back of the hand and foot; 2685 on the sole of the foot; and 2736 on the palm of the hand. The total number of the sudoriparous glands, without reckoning those of the axilla, is estimated (somewhat too highly) by Krause at 2,381,248, and their collective volume (with those of the axilla), at 39,653 cubic inches.

The *vessels* of the sudoriparous glands are particularly well seen in those of the axilla (fig. 78); in others, the vessels may also be seen here and there (best in the *penis*, where, for example, glands of 0·36‴ are supplied by the most delicate ramifications of an artery of 0·06‴, in their interior); and in successful injections of the skin, the glands appear as reddish corpuscles. *Nerves* have not hitherto been found in them.

§ 67.

Intimate structure of the glandular Coil.—The sudoriparous glands, in general, consist of a single much convoluted canal (in one case, according to Krause, $\frac{3}{4}$‴ long), twined into a coil, which retains pretty nearly the same diameter throughout its length, and terminates, either upon the surface of the coil, or in its interior, in a slightly enlarged blind extremity. In the large glands of the axilla alone, the canal is usually divided, dichotomously, into branches, which subdivide, and sometimes, though rarely, anastomose; and after giving off small cæcal processes, each separate branch finally terminates in a blind extremity. The glandular canals have either *thin* or *thick* walls (fig. 79). The former (fig. 79, *A*) possess an external fibrous investment, consisting of indistinctly fibrous connective tissue, with scattered elongated nuclei; internally this is sharply limited, perhaps by a *membrana propria*, and is covered by a single, double, or multiple layer of polygonal cells of 0·005—0·007‴, which in their chemical relations and otherwise, correspond perfectly with the deep cells of pavement-epithelium, except that they almost invariably contain a few

fatty granules, and still more frequently a small quantity of yellowish or brownish *pigment-granules.*

The thick-coated sudoriparous glandular canals (fig. 79 *B*)

Fig. 79.

possess, besides the two layers just described, a middle layer of smooth muscles running longitudinally, whose elements are easily separable, as muscular fibre-cells of 0·015—0·04‴ long, 0·002—0·005, or even 0·008‴ broad, occasionally, with a few pigment-granules, and each containing a roundish elongated nucleus. Whenever the glandular tubes contain only fluid, the epithelium is a single very distinct layer of polygonal cells of 0·006—0·015‴; in the opposite case it can be seen only with difficulty, or not at all. With respect to the occurrence of these two forms of glandular canals, the thick muscular walls are found, especially in the large glands of the axilla, whose cells all possess muscular walls, and thence acquire a very peculiar striated appearance. I have noticed a precisely similar structure only in the large glands of the root of the *penis* and of the nipple, although it is true that there is occasionally a muscular development, but slighter and only partial, in the glands of the palm, whose wide canals are distinguished by the thickness of their walls, and exhibit a muscular structure dis-

Fig. 79. Sweat ducts, × 350. *A*, one with thin walls and a central cavity, without a muscular coat, from the hand: *a*, connective investment; *b*, epithelium; *c*, cavity. *B*, a portion of a canal without a cavity, and with a delicate muscular layer, from the *scrotum*: *a*, connective tissue; *b*, muscular layer; *c*, cells, which fill the glandular canal with yellow granules among their contents.

tinctly enough, though thinner than elsewhere. The same description applies to certain glands of the *scrotum*, and even of the back, of the *labia majora*, of the *mons veneris*, and of the neighbourhood of the *anus;* yet with this limitation, that often only a small part of the glandular tube, perhaps merely its cæcal extremity, is provided with a muscular coat. The glands of the leg, of the *penis*, of the *thorax* (the *areola* excepted), of the eyelids, and the majority of those of the back and thigh, of the chest and abdomen, as well as of the two prominent segments of the upper extremity, are delicate and without muscles.

The diameter of the glandular canals varies, in the smaller glands from 0·022—0·04‴, and is about 0·03‴ on the average; the thickness of the walls, 0·002—0·003‴; of the epithelium, 0·006‴; of the cavity, 0·004—0·01‴. Among the axillary glands some have canals of 0·07—0·1‴, even 0·15‴, with walls 0·006‴ in thickness, without the epithelium, the half of which is formed by the muscular layer; others, and in fact the largest glands, possess canals of 0·03—0·06‴, with walls of 0·004‴; in the *areola* and the *genitalia*, also, the dimensions of the larger glands vary, though within narrower limits.

All the coils of the sudoriparous glands are penetrated by connective tissue, interspersed with fat cells, which supports the vessels and unites the separate convolutions of the tubes with one another; some of them have an external fibrous covering investing the whole coil (of common connective tissue with fusiform nuclei), which is particularly well developed in those more isolated coils which are lodged in the subcutaneous cellular tissue (*penis, axilla*, &c.)

§ 68.

Secretion of the sudoriparous Glands.—All the smaller sudoriparous glands contain, as soon as any cavity is apparent in their canals, which, however, is by no means always the case, nothing but a clear, bright fluid, without any formed contents. In the axillary glands, on the other hand, the contents abound in formed particles, and appear either as a greyish, transparent, semi-fluid substance, with innumerable fine, pale granules, and often with solitary nuclei; or as a whitish-yellow, tolerably viscid matter, with a varying quantity

of larger, opaque, colourless or yellow granules, nuclei and cells, similar to the epithelial cells above described. That these contents, which, as I have found, contain much protein and fat, differ considerably from the common *sweat*, which is fluid and presents no formed elements, and probably rather approximate to the sebaceous secretion of the skin, is evident, on which account we might be induced to remove the glands of the axilla from the class of sudoriparous glands, and to regard their secretion as of a peculiar kind. These glands, however, sometimes afford a secretion containing but few granules, or even nothing but fluid; and among the larger axillary glands smaller ones occur, which, so far as regards their contents, exhibit many transitions, on the one hand into the large, and on the other into common small glands. If we further consider that, occasionally, the sudoriparous glands in other situations, as, for instance, in the *areola* of the nipple, contain a fluid abounding in granules, it is clear that it is unadvisable to distinguish the large axillary glands from the common kind, on account of the difference in their secretion; and the more so, indeed, because we by no means know whether the latter, under certain circumstances, may not contain granules.

As respects the origin of the granular contents, they must be referred to the cells which are developed in the glandular tubes. For we frequently meet in these with cells containing the same granules, which also occur free within the glandular canals; and frequently may be said to constitute their whole contents. It sometimes happens, also, that in one and the same gland the ends of the glandular tubes contain nothing but cells, while the excretory duct exhibits hardly any trace of them, presenting merely granules and scattered free nuclei; and in this case we can easily see that the cells, as they pass further upwards, become broken up to a greater and greater extent, thus setting free their nuclei and the granules in their interior. These cells plainly proceed from the epithelial cells lining the canal of the sudoriparous coil; for, in the first place, the cells of the contents and the epithelium resemble one another in all respects; and secondly, where cellular or granular contents are found in the glands themselves, the epithelium is for the most part completely absent, so that the former rests immediately

upon the muscular membrane. Now, since on the other hand, in those glands which contain only a clear fluid, the epithelium is always easily seen, and often presents many dark (even golden yellow) pigment-granules in its cells, it may perhaps be assumed, that the cells in the contents are nothing but detached epithelium, and that the secretion mainly depends upon a growth and continual casting off of the epithelial cells.

[The examination of the secretion of the sudoriparous glands is neither chemically nor microscopically complete. As regards the former, the fact that the axillary glands secrete fat and a nitrogeneous substance in large quantities, appears to me interesting, since from the obvious similarity in structure between these and the other sudoriparous glands, we may perhaps draw some conclusions as to the secretion of the latter. We already know that the ordinary perspiration contains nitrogenous matters (extractive); and as Krause (l. c., p. 146) has clearly shown, fat also; and it may be asked whether these substances do not perhaps in certain situations (*e. g.* hand, foot) occur more abundantly, or under certain conditions (local, adhesive, peculiarly odorous perspiration) increase in quantity. The so-called sweat-corpuscles of Henle (l. c., pp. 915 and 939), that is, structures similar to the mucous corpuscles, I have hitherto found neither in the sweat of man nor in the smaller glands; but I may remark that almost constantly, even in the smaller sudoriparous glands, certain canals exist which present no cavity, but are wholly filled with epithelial cells. These appeared to me always to be near the blind end (fig. 79, *B*), whilst those which are nearer the excretory duct, almost invariably exhibit a cavity 0·004—0·1‴ in diameter. I consider it therefore to be not impossible, that in the common sudoriparous glands, a cellular secretion is at times formed and excreted in the same manner as in the axillary glands; for from what we see in the canals of the latter, it can hardly be doubted that granules, nuclei, and perhaps also remains of cells, occur in the sweat of the axilla. Whether the sweat in different individuals and races of men present notable differences is unknown, for it is not ascertained that the different odour of the cutaneous exhalation in the European and the Negro, for instance, depends on the sweat or the material of the per-

spiration; nor have its pathological relations been investigated, at all events not microscopically.

§ 69.

Sweat-Ducts.—The excretory ducts of the sudoriparous glands, the *sweat-ducts*, or *spiral-canals* (figs. 45, 80), commence at the upper end of the glandular coil as simple canals, ascend with slight undulations vertically through the *corium*, and then penetrate between the *papillæ* (never through their points), into the epidermis. Here they begin to twist, and according to the thickness of the cuticle they perform from 2—16 closer, or more distant spiral turns, until eventually they terminate by small, round, often funnel-shaped apertures, the so-called *sweat-pores* on the free surface of the epidermis.

Fig. 80.

The length of the sweat-ducts depends on the situation of the glands and the thickness of the skin. The commencement of the duct is invariably narrower than the canal in the coil itself, measuring 0·009—0·012‴; it continues narrow up to its entrance into the *stratum Malpighii*, where it dilates to about double the size, *i. e.*, to 0·024—0·028‴ (fig. 80); retaining this breadth, it traverses the epidermis, and terminates in an aperture of $\frac{1}{50}$—$\frac{1}{20}$‴. In the axillary glands, the excretory duct measured in one case at the level of the sebaceous glands 0·06—0·09‴, immediately under the *epidermis* 0·03‴, in the *epidermis* itself

Fig. 80. Perpendicular section through the epidermis and outer surface of the corium of the bulb of the thumb, transversely through two ridges, × 50, and treated with acetic acid: *a*, horny layer of the epidermis; *b*, mucous layer; *c*, cutis; *d*, simple papilla; *e*, compound papilla; *f*, epithelium of a sweat-duct passing into the mucous layer; *g*, cavity of it in the cutis; *h*, in the horny layer; *i*, sweat-pore.

0·06‴. In the *corium* the sweat-ducts have always a distinct cavity, an external investment of connective tissue, with elongated nuclei (in the glands of the axilla, muscles also), at all events inferiorly, and an epithelium composed of at least two layers of polygonal, nucleated cells without pigment granules. Where the ducts enter the epidermis, they lose their investment of connective tissue, which coalesces with the outermost layer of the *corium*, and henceforward they are bounded by nothing but layers of cells, which in the *stratum Malpighii* are nucleated, but in the horny-layer are without nuclei. Chemically and morphologically they completely resemble the epidermic cells, with the sole exception that they are disposed more perpendicularly, particularly in the horny-layer. The duct has often a distinct cavity in the *epidermis*, at other times there is a granular streak in the place of it, which is probably either a secretion or a deposit from the secretion. The *sweat-pores*, whose disposition, corresponding with that of the glands, is sometimes very regular, at others more irregular, are distinguishable, even with the naked eye, in the palm of the hand and sole of the foot. In other localities they are visible only with the aid of the microscope; occasionally the excretory ducts of two glands unite into a single canal (Krause).

§ 70.

Development of the sudoriparous Glands.—The sudoriparous glands first appear in the fifth month of embryonic life, and are originally *perfectly solid, slightly flask-shaped, processes of the stratum Malpighii of the epidermis*, and are very similar to the first rudiments of the hair-sacs. In the earliest condition which I have observed, the processes measured in the sole of the foot 0·03—0·09‴ in length, and 0·01‴ in breadth at the neck, at the bottom 0·018—0·02‴, and even the very longest did not penetrate more

Fig. 81.

Fig. 81. Rudiment of a sudoriparous gland of a human embryo at five months, × 350: *a*, horny layer of the epidermis; *b*, mucous layer; *c*, *corium*; *d*, rudimentary gland as yet without any cavity and consisting of small round cells.

than half through the cutis, which was 0·25‴ thick. They were entirely composed of round cells, perfectly similar to those of the *stratum Malpighii* of the epidermis; besides which, each process had a delicate investment, which was continuous with the boundary of the inner surface of the *epidermis.* No trace of sweat-pores or ducts was visible.—At the beginning of the sixth month, the glands in the sole of the foot and palm of the hand extend as far as the middle and inner fourth of the *cutis,* measure at the clavate extremity 0·028—0·04‴ and 0·016—0·02 in the duct which arises from them, are already slightly serpentine, and present a cavity, at all events partially, in their narrow portion; they do not, however, penetrate the cuticle, or in any way open on the surface. It was not before the seventh month that I perceived, in the same situations, the first indications of the sweat-pores and ducts in the *epidermis,* though as yet very indistinct, and the latter forming only half a spiral turn (fig. 82, *A*); at the same time the part of the gland which projected into the *corium* was more considerably developed, reached as far as the innermost portion of that structure, and at its cæcal extremity was bent into a hook or even slightly convoluted, so as to afford the first indication of a glandular coil of about 0·04 to 0·06‴. The canal arising from it usually presented several marked undulations and measured in total thickness 0·015—0·022‴, with a cavity of 0·003—0·004‴, which frequently extended even to the ter-

Fig. 82.

Fig. 82. *A*, rudiment of a sudoriparous gland from a seven-months' fœtus, × 50. The letters *a*, *b*, *d*, as in fig. 81. The cavity *e* is present throughout, only it does not extend quite so far as the end of the thicker part of the rudiment of the gland, which becomes converted into the glandular coils. The continuation of the canals into the epidermis and the sweat-pores, *f*, are present. *B*, a coil of a sudoriparous gland from a fœtus at the eighth month.

minal coil: like the latter it was composed of the original though thickened membrane continuous with the surface of the corium, and of an *epithelium* consisting of many layers of pale, polygonal, or rounded cells. The glands of the rest of the body, about this period, appeared to me to be similarly constituted. I can say nothing as to their earlier condition, but even those of the axilla were in no wise distinguished from the rest. From this time the development goes on very rapidly; the end of the gland elongates more and more, and coils itself up (fig. 82 *B*), so that it assumes an appearance hardly different from that which it presents in the adult. In the new-born infant, the glandular coils in the heel measure 0·06—0·07‴ (in a child of four months 0·06—0·1‴ on the heel, in the hand 0·12‴), present much convoluted canals of 0·015—0·02‴, and traverse the epidermis with their already twisted ducts (in the corium of 0·008‴, in the *rete Malpighii* of 0·022‴).

It results from these facts that the sudoriparous glands are nothing else than involutions of the skin, and do not begin as hollow structures, but are at first a simple development of the *stratum mucosum*. By a continual process of cell-multiplication, the original rudiments grow deeper and deeper into the skin, acquire their peculiar spiral windings, and divide into the glandular coil and the sweat-duct; while at the same time, either by liquefaction of their central part, which would thus, as it were, represent a first secretion, or by the excretion of a fluid between their cells, a cavity is produced. How the sweat-duct in the *epidermis* and the pore are formed is doubtful; probably by a formative process in the *epidermis* itself. According to a few measurements which I have instituted ('Mikroscop. Anat.,' II, i, 171), a development of sudoriparous glands appears to take place even after the fifth month, whilst the whole number appears to exist at birth.

[Little is known as to the *pathological* conditions of the sweat-glands. Kohlrausch (Müller's 'Archiv,' 1843, p. 366), has found them of considerable size ($\frac{1}{2}$‴) in an ovarian cyst, together with hairs and sebaceous follicles. In *Elephantiasis graecorum*, G. Simon and Brücke (Simon, 'Hautkrank.,' p. 268), noticed an increase in size of the sudoriparous glands, and V. Bärensprung observed the same thing in a kind of

wart (l. c., p. 81); the latter also found that these glands were atrophied in corns, and that the duct in the outer layers of the *epidermis* had disappeared. The condition of the several glands in old age, in cases where the secretion of sweat is altogether wanting, and in abnormal perspirations, is not known. In a remarkable case of *Ichthyosis congenita* (very similar to that mentioned by Steinhausen, only more marked) in a new-born infant, which was examined by Dr. H. Müller and myself, the sudoriparous glands were present; their excretory ducts, so far as regards their course through the *epidermis*, which was thickened to 2‴, were partly disposed as usual, partly they were placed, as in the sole of the foot, with their outer portions almost completely horizontal, and ran in some places for as much as $1\frac{1}{2}$‴ in this manner, so that in superficial sections of the *epidermis* they appeared as parallel, at first sight altogether abnormal canals, with a cavity of 0·0025—0·003‴. The contents of the ducts were very peculiar, consisting invariably of a multitude of white oil drops. I observed sudoriparous glands also in the case described by Mohr, of a great cavity containing hairs, in the lung ('Berlin Med., Central-zeitung,' 1839, No. 13), they were about 0·24‴ in diameter, and were contained in a *panniculus adiposus*, with common fat-cells; and it may be remarked that the wall of the cavity besides the *panniculus* also presented a *corium* with papillæ, and an *epidermis* like the external integument.

Method of investigation.—To examine the position of the sudoriparous glands and their excretory ducts, fine sections of fresh or slightly-dried skin of the palm or sole should be prepared, and made transparent by acetic acid or caustic soda. Gurlt used for this purpose skin hardened and rendered transparent in a solution of carbonate of potass (*liquor kali carbonici*). Giraldès macerates the skin for twenty-four hours in dilute nitric acid (1 part acid, 2 parts water) and for twenty-four hours in water,—a process which, according to Krause, is very useful, as the glands become yellow, and are readily distinguished. In macerated pieces of the skin, the cellular lining of the sweat-ducts may be drawn out of the corium, in the form of long tubes, with the *epidermis*; in delicate parts of the skin I have, not unfrequently, succeeded in doing this after treatment with concentrated acetic acid.

The investigation of the glandular coils themselves is very easy in the axillary glands; in the others the skin must be prepared from within, and the glands sought for partly upon the inner surface of the cutis, partly in its meshes,—a method which readily succeeds, with a little attention, particularly in the hand, foot, and nipple. The large glands of the ball of the foot of the Dog, described by Gurlt, are particularly well fitted for demonstration, and still more those of the prepuce and of the integument of the udder of the Horse, which lie quite loose in the subcutaneous tissue. If it be desired to count the glands, their apertures may be sought for, or a piece of skin of determinate size may be treated according to Giraldès' method, and examined portion by portion (Krause). For the study of the development of the glands, sections of the fresh and dried skin of the heel and palm of embryos, may be made with the double knife or razor. In embryos preserved in spirit, if the sections be fine, the glands may also be very well seen, especially in the first moments of the action of caustic soda.

Literature.—Breschet et Roussel de Vauzème, 'Recherches anatomiques et physiologiques sur les appareils tégumentaires des animaux,' in the 'Annales des Sciences Nat.,' 1834, pp. 167 and 321 (discovery of the sudoriparous glands); Gurlt, 'Vergleichende Untersuchungen über die Haut des Menschen und der Haussäugethiere, besonders in Bezug auf die Absonderungsorgane des Hauttalges und des Schweisses,' in Müller's 'Archiv,' 1835, p. 399 (first good figures of the glands themselves). Besides these, compare especially the general works of Todd and Bowman, Henle, Valentin, Hassall, and myself; the above-cited treatises of Krause, myself, Simon, Von Bärensprung, and Wilson; further the figures of Berres, tab. XXIV; R. Wagner, 'Icon. Phys.,' tab. XVI, fig. 9; F. Arnold, 'Icon. Org. Sens.,' tab. XI; and my own 'Mikr. Anat.,' tab. I.

B. OF THE CERUMINOUS GLANDS.

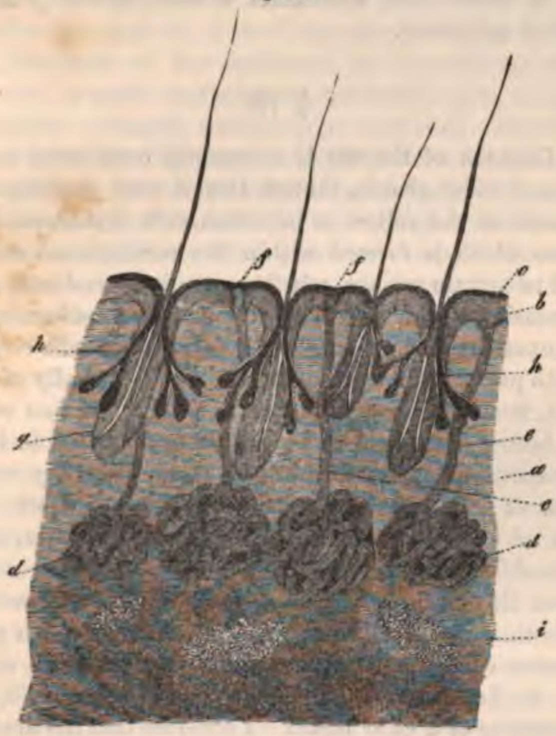
§ 71.

The ceruminous glands of the Ear are brownish simple glands, in external appearance precisely similar to the sudoriparous glands, which do not exist in the whole external auditory *meatus*, but only in its cartilaginous portion, where they are situated between the lining membrane of the passage and the cartilage, or the fibrous substance which supplies its place, in a tough subcutaneous tissue, containing little fat. They form a connected yellowish-brown layer, visible enough to the naked eye, which is thickest in the inner half of the cartilaginous *meatus*, and becomes gradually thinner and more lax externally, extending, however, quite as far as the cartilaginous *meatus* itself. Each ceruminous gland consists of a glandular coil and an excretory duct. The former (fig. 83 *d*), $\frac{1}{10}'''$—$\frac{1}{4}$—$\frac{3}{4}'''$ in size, is formed by the multitudinous convolutions of a single canal of 0·03‴—0·06‴, on the average 0·04‴—0·05‴ thickness, which occasionally, although not constantly, throws out little diverticula, and terminates in a blind slightly enlarged end. From the coil a short straight excretory duct, 0·017—0·024‴ thick, passes perpendicularly upwards, penetrates the *corium* and epidermis of the auditory *meatus*, and usually opens independently in a circular pore of 0·044‴, or else into the upper part of a hair sac.

The following is the intimate structure of the ceruminous glands. The canals of the coil present a fibrous coat and an epithelium, the former being 0·004—0·005‴ in thickness, the latter 0·004‴. The fibrous covering presents exactly the same conditions as in the larger sudoriparous glands, that is, it consists of an internal longitudinal layer of smooth muscles, 0·0023—0·0026‴ in diameter, and an external layer of connective tissue, with scattered nuclei, and occasionally very fine transverse nucleus fibres. The *epithelium* rests immediately upon the muscular layer, and consists of polygonal cells of 0·006—0·01‴ in a single layer, which contain a greater or smaller number of yellowish-brown pigment granules, of immeasurable minuteness, insoluble in acids and alkalies in the

cold, or whitish fat-globules up to 0·001‴ in size, and which are so disposed that whole lengths of a gland contain generally

Fig. 83.



only one and the same kind of granules; whence it arises that they appear either uniformly brownish or opaque (by reflected light whitish). The contents of the glandular canals are sometimes a clear fluid, sometimes a granular substance composed principally of cells analogous to those of the *epithelium*, whence it would seem that the same kind and mode of secretion occurs in them as in the sudoriparous glands. The excretory ducts possess a coat of connective tissue, and an

Fig. 83. Perpendicular section through the skin of the external auditory meatus, × 20: *a*, corium; *b*, *stratum Malpighii;* *c*, horny layer of the *epidermis;* *d*, coil of the ceruminous glands; *e*, their excretory ducts; *f*, their apertures; *g*, hair-sacs; *h*, sebaceous glands of the meatus; *i*, masses of fat.

epithelium consisting of several layers, and constituted of small nucleated cells, without fat or pigment granules. In their cavity, which is, however, not always distinct, they sometimes contain a clear fluid, sometimes a small quantity of finely-granulated substance.

§ 72.

The *Cerumen* of the ear is commonly considered to be the secretion of these glands, though this is only partially correct. If we examine the yellow or brownish, soft or more solid, viscid substance which is formed within the cartilaginous meatus, it is found to contain various constituents: independently of a few hairs, occasionally an *Acarus folliculorum*, and epidermic cells in various numbers, there occur,—1. Very many cells completely filled with pale fatty matter of 0·009—0·02‴, usually of an oval, flattened, irregular shape; in which, on the addition of water, or still better of caustic soda, the fat is separated in isolated, round, or irregular dark drops. 2. Much free fatty matter in the form of pale, small yellowish round drops, which, on the addition of water, appear as dark spherical granules, from an immeasurable minuteness up to 0·002‴ and more; and it is only upon this addition that they become quite distinct, but at the same time are decolorised. 3. Yellow or brownish granules and masses of granules, free or rarely in cells, few upon the whole. 4. Lastly, when the secretion is more fluid, also a small quantity of a clear liquid. I consider that the first-named cells belong to the sebaceous secretion of the external meatus; but that the remainder is the secretion of the ceruminous glands, which would therefore eliminate oily fluid with scattered brown granules. This being the case, the analysis by Berzelius of the common ear-wax, a mixture of the sebaceous and proper ceruminous secretion, must only be admitted with caution. In my opinion, the brownish-yellow bitter substance, soluble in alcohol and water, found by him, and the pale yellow strong tasted extractive matter, hardly soluble in water and not at all in alcohol, must be attributed to the ceruminous glands; the remaining fat, the horny matter, and probably also most of the albumen, to the sebaceous glands; whilst the relations of the salts must, of course, be left undetermined.

The vessels of the ceruminous glands are disposed like those of the sudoriparous; in one case I noticed, in addition, a fine nervous fibre of 0·003‴ in the midst of a gland. As to the development of these glands I can only say, that in a fœtus of five months they had the form of straight, pale processes of the *stratum Malpighii* of the epidermis of the external auditory *meatus*, were entirely composed of nucleated cells, and ended by a slightly enlarged termination somewhat twisted upon its axis, in which the first indication of a glandular coil was presented. In other words, these rudimentary glands exactly resembled the sudoriparous glands at the same period; and considering the great anatomical resemblance between the two structures, I do not doubt for a moment that the ceruminous glands, both in their first commencement and subsequently, go through the same phases as the former.

[According to all that I have seen of the ceruminous glands, I must consider them to be mere modifications of the sudoriparous. In speaking of these it has already been remarked, that their secretions are certainly not everywhere identical, being in one locality more aqueous, in another fatty and albuminous, with peculiar odorous ingredients. Even although the *cerumen* may, to some extent, contain peculiar substances, *e. g.*, the yellow bitter substance, which, however, according to Lehmann, is not bilin, nevertheless, taking into account the other correspondences (consider the almost constant and often very abundant yellow granules in the sudoriparous glands, which are also insoluble in acids and alkalies), we may associate the ceruminous glands with the sudoriparous, especially with the larger among the latter, which are both anatomically and physiologically most closely allied to them; in fact, I am inclined, for my own part, to think, that the smallest pale ceruminous glands at the commencement of the meatus are hardly distinguishable from common sudoriparous glands. Nothing is known of the pathological conditions of the ceruminous glands—of the *cerumen* itself we know that it is often quite solid, at other times fluid, puriform, and pale coloured. In the latter case, which is seen in congested conditions of the external meatus, it contains far more fluid and free fat than

usual, and very beautiful cells containing fat.[1] With regard to the mode of examining the ceruminous glands, I must refer to the sudoriparous glands, with which they wholly agree in position, chemical relation to acids, alkalies, &c. &c.

Literature.—R. Wagner, 'Icones Phys.,' tab. xvi, fig. 11, *A, B*; Krause and Kohlrausch, in Müller's 'Archiv,' 1839, p. cxvi; Pappenheim, 'Beiträge zur Kentniss der Structur des gesunden Ohres,' in Froriep's 'Neue Notizen,' 1838, No. 141, p. 131, and Specielle Gewebelehre d. Gehörorgans (Breslau, 1840); Henle, 'Allg. Anat.,' pp. 915, 916, 934, 941; Huschke 'Eingeweidelehre,' p. 819; Hassall, 'Microsc. Anatomy,' &c., p. 427, pl. lvii; Valentin, article 'Gewebe,' in Wagner's 'Handw. d. Phys.,' i, p. 755.

C. OF THE SEBACEOUS GLANDS.

§ 73.

The *sebaceous Glands* are small whitish glands, which exist in almost every part of the skin, and which afford the cutaneous sebaceous or fatty secretion.

In *form* they vary very considerably; the simplest (fig. 84, *A*) are short follicles of an elongated or pyriform shape; in others—the *simple racemose glands*—two, three, or even more follicles or vesicles are united with a shorter or longer peduncle; whilst in others, lastly (figs. 84 *B*, 85), two, three, or more simple clusters of follicles communicate with a common duct, constituting an elegant *compound racemose gland.* Besides

[1] [There is an occasional ingredient in the so-called *cerumen* which is worthy of notice, viz. a mucedinous fungus. Attention has been recently called to its occurrence by Dr. Inman ('Quarterly Journal of Micros. Science,' January, 185 states that a pellet of ear-wax which he examined was composed of
fungus, with a minute portion of epithelium. However, Professor
so long ago as 1844 ('Beobachtung von Cysten mit Fadenp
Gehörgange,' &c., Müller's 'Archiv,' 1844, p. 404), described
of certain sacs containing fungi, which were tracted fr
meatus of a girl eight years old,—in whor ey
companied by considerable deafness and
and open at one end; externally they
from which mucedinous threads, te
the cavity of the sac. These sacs
charged, to a very considerable

these three forms, which represent only the chief varieties, there are a good many intermediate ones, which do not require any detailed description.

Fig. 84.

The sebaceous glands occur principally in the hairy parts of the body, opening, in common with the hair-sacs, upon the surface, whence they have also been termed *the glands of the hair-sacs.*

In all the coarser hairs, the glands appear to be lateral appendages of the hair-sacs, and open by narrow excretory ducts into them (figs. 75, 76, 77, 83), whilst in the *lanugo* the ducts and the hair-sacs are often of about the same diameter (fig. 84 *B*), and open into a common canal, which may be regarded as a continuation of the one as much as of the other; or the ducts may even be the larger (fig. 85), the hairs bearing a subordinate relation to them, so that their sacs open into the glands, and the hairs come out through the glandular opening itself. In the *hair-less parts* of the surface, sebaceous glands occur only in the *labia minora* (*vide* § 54), and in the *glans penis* and prepuce, whilst they do not exist in the *glans* and prepuce of the *clitoris*. In general, the glands are situated close to the hair-sacs in the superficial layer of the *corium*, and are larger in the finer hairs than in the coarser; in *particular* cases, however, they present many differences. With respect to the glands of the larger hair-sacs, they are usually of the

Fig. 84. Sebaceous glands from the nose, × 50: *A*, simple tubular gland without any hair; *B*, compound gland, which has a common opening, with a hair-sac: *a*, glandular epithelium, connected with *b*, the *stratum Malpighii* of the *epidermis*; *c*, contents of the glands, sebaceous cells, and free fat; *d*, the separate racemes of the compound gland; *e*, hair-sacs (root-sheath), with the hair, *f*.

simple racemose kind, having an average size of $\frac{1}{10}$—$\frac{3}{10}'''$, and are disposed around the sac to the number of from 2 to 5. The smallest, of 0·1—0·16″, occur in pairs, attached to each hair of the scalp; they are somewhat larger, 0·16—0·24, in the hairs of the beard, and the longer hairs of the chest and *axilla*, in which situations several glands are usually disposed around the hair follicle; the largest of all exist on the *mons veneris*, the *labia majora*, and the *scrotum*, where, at all events in the last-mentioned locality, they are found at the deepest boundary of the *corium*, and the glands, from four to eight being connected together, represent beautiful rosettes $\frac{1}{4}$—$\frac{1}{2}$—1‴ broad.

Fig. 85.

Attached to the sacs of the smaller coarse hairs, I find smaller sebaceous glands of 0·06—0·24‴, mostly in pairs; and also in the eyebrows, eyelids, and the hairs at the entrance of the nostrils. The lanuginous hairs have generally larger glands, or aggregations of glands, of $\frac{1}{4}$—1‴; these are best displayed in the nose, the ear (*concha*, *fossa scaphoidea*), the *penis* (anterior half), and the *areola mammæ*, especially in the first of these situations, where the glands often attain a colossal size, and altogether peculiar forms (fig. 85); the glands generally have a diameter of $\frac{1}{5}$—$\frac{1}{3}'''$ on the *caruncula lachrymalis*, the lips, brow, thorax, and abdomen; they are somewhat smaller, $\frac{1}{5}$—$\frac{1}{6}'''$, but almost always larger than in the hairs of the scalp, in the eyelids, cheeks, neck, back, and extremities. Of the glands which are not connected with hair-sacs, only a portion of those of the *labia minora* are of large size (0·14—0·5‴) and rosette-shaped, with aperture of 0·033‴; the others are for the most part simply tubular, and at most 0·12—0·16‴ long,

Fig. 85. A large gland from the nose, with a little hair-sac opening into it, × 50 The letters *a*—*f* as in fig. 84.

0·04—0·06‴ broad. The *glandular vesicles* of the sebaceous glands are either round, or pyriform and flask-shaped, or even elongated or tubular. Their size varies exceedingly, from 0·06—0·16‴ in length, 0·02—0·1‴ in breadth, and is in the mean 0·04‴ in the round ones; 0·08‴ in length, 0·03‴ in breadth in the others. The excretory ducts also have very different dimensions, sometimes long, sometimes short, broad or narrow; the principal excretory ducts measure in the nose and *labia minora* up to $\frac{1}{3}$‴ in length, $\frac{1}{15}$ — $\frac{1}{8}$‴ in breadth, and have an epithelium 0·015—0·03‴ thick.

[The sebaceous glands on the *glans penis*, and on the inner lamella of the prepuce or 'Tyson's glands,' are very inconstant, occurring sometimes only in a very small number, sometimes in hundreds. They are ordinary sebaceous glands, which are distinguished from those of other regions by their not being connected with hair-sacs, and by their opening independently on the surface of the skin. They may, generally, be perceived by the naked-eye, as small whitish points which do not project above the skin; and in sections of skin, treated with caustic soda or acetic acid, their peculiarities may be readily studied with the microscope. They appear to be sometimes tubular, at others simply racemose; the former present a round or pyriform follicle of 0·048—0·12‴ in diameter, and a straight excretory duct of $\frac{1}{10}$‴ in length, and 0·024—0·035‴ breadth; the latter have 2—3, or at most 5, terminal vesicles, and measure 0·08—0·18‴ altogether. The aperture of both kinds of glands, which have a diameter of 0·02—0·06‴, are easily seen. With regard to the position of the

Fig. 86.

Fig. 86. Two sebaceous glands; the larger, 1, from the inner lamella of the prepuce; the smaller, 2, from the glans penis, × 50: *a*, glandular epithelium continued into the *stratum Malpighii* of the skin; *b*, *c*, contents of the gland, with scattered larger fat-drops; *g*, horny layer of the epidermis projecting somewhat into the duct.

glands, I would remark that I have never failed in finding them, 10—50 and more, in number, on the inner lamella of the prepuce, especially in the neighbourhood of the *frænulum*, and its anterior part; while on the glans itself and its neck, they are sometimes totally absent, sometimes they occur on its anterior surface, and then generally in great numbers (up to 100). On the prepuce, the glands are for the most part racemose, in the *penis* more simple. Their contents exactly resemble those of the sebaceous glands, viz. cells containing fat, of which more will be said below.

The sebaceous glands of the external sexual organs in the female, are found, generally in great numbers, on the inner and outer surface of the *labia minora*, and some of them are as large as those belonging to the fine hairs on the *labia majora*, while some are smaller. I have never found sebaceous glands in the *glans* and inner lamella of the *præputium clitoridis*, although Burkhardt speaks of such in the *corona clitoridis*, but, in a few instances, I have met with them about the *urethra* and the entrance of the *vagina*. Resembling the sebaceous glands in all essential points, except their larger size, are the *Meibomian glands* in the eyelids, of which a more particular description will be given when we treat of the eye.

According to E. H. Weber (Froriep, 'Notiz.,' Marz, 1849), the *smegma preputii* of the Beaver, the 'Castor,' is not, in the main, a glandular secretion, since only a small portion of the pouch in which it is secreted is furnished with very simple, rounded, lenticular glandules, the largest measuring $\frac{1}{33}'''$. The secretion, in individuals of both sexes, may rather be described as a laminated substance lining the entire 'castor-pouch,' and consisting merely of epidermic-cells and minute fatty globules. Leydig ('Zeitsch. f. w. Zool.,' Bd. II, pp. 22, 31, et seq.), finds no glands at all in the 'castor-pouch;' and according to him, the same is the case in the preputial sac of the Weasel, whilst in the Rat and Mouse, the prepuce contains true sebaceous glands of a complicated structure

§ 74.

The minute structure of the sebaceous glands may be described as follows:—Each gland possesses an external delicate coat of connective tissue, continued from the hair-sac, or,

in the case of free glands, from the *corium*, and containing masses of cells, which exhibit different conditions according to the part of the gland. If we proceed from the excretory duct of one of them (fig. 88 *B*), we see, that not only the fibrous coat of the hair-sac, but a portion of its inner root-sheath also, passes into the duct, and lines it with nucleated, rounded, or polygonal cells, disposed in several (two to six) layers. This cellular layer is continued, becoming more and more delicate, into the remoter parts of the gland, and ultimately penetrates into the proper glandular vesicles, clothing them with a single, rarely a double, layer. Internally to these cells, which are distinguished by a greater or smaller number of fat granules from the epithelial cells above them, there immediately succeed, in the glandular vesicles themselves, others (fig. 87 *B b*) containing more fat; and these finally pass into the innermost cells of the glandular vesicles, which are invariably larger (of 0·016—0·028‴) than the middle and outermost cells, are rounded or elongated in their form, and so filled with colourless fat that they might, not improperly, be termed sebaceous cells (fig. 87 *B*). The fat contained in them appears, either still to retain the form of discrete drops (*bb*), as in the outer cells, or, as is indeed more frequently the case, under that of larger drops; and in many cells there are but a few of them, or even only a single one, which quite fills the cell (*d*); in consequence of which these cells greatly resemble the fat-cells of the *pan-*

Fig. 87.

Fig. 87. *A*, a glandular vesicle of a common sebaceous gland, × 250: *a*, epithelium sharply defined, but without any investing *membrana propria*, and passing continuously into the fat-cells, *b* (their contours are too indistinctly drawn), in the interior of the glandular tube. *B*, sebaceous cells from the glandular tube, and the cutaneous sebaceous matter, × 350: *a*, smaller nucleated cells, still, more of an epithelial character, and containing but little fat; *b*, cells abounding in fat, without visible nucleus; *c*, cell, in which the fat is beginning to flow into one mass; *d*, cell with one fat-drop; *e*, *f*, cells from which the fat has partially escaped.

niculus adiposus. If these innermost cells, which rarely exhibit any nucleus, are traced onwards towards the excretory duct, nothing is more easy to observe, than that similar cells, applied uninterruptedly one to the other, are continued into this also, *i. e.*, into the canal lined by its *epithelium;* then, entering the hair-sac, they occupy the space between the hair and the epidermis of the hair-sac, and are finally extruded. These cells are the sole sources of the cutaneous sebaceous matter, a substance which, when fresh and at the common temperature, is semifluid, but in the dead subject more consistent, like butter or soft cheese, whitish or whitish-yellow in colour, sometimes viscid, at others friable. Its cells, in the fresh secretion, adhere together more or less closely, and are thence generally flattened and irregular in form; their membrane is not recognisable, and their contents are quite homogeneous, and transparent, with a yellowish hue. If dilute alkalies, however, be added, they swell up after a short time into beautiful round or elongated vesicles, in which, in consequence of the penetration of the reagent, the fat divides into separate drops of various sizes, and into irregular masses; at the same time the sebaceous matter becomes white, owing to the numerous minute fatty particles which are produced, and larger fat drops are formed, probably in consequence of the solution of many cells. Besides that in the cells, the sebaceous matter also contains *free fat,* in larger or smaller quantity, and in some cases, perhaps, an excessively minute amount of a clear fluid.

It appears, then, that the cutaneous sebaceous matter is a secretion, consisting, so to speak, only of formed elements, either cells containing fat alone, or cells together with drops of fat. These constituents are formed in the vesicular ends of the glands, in consequence of a production of cells, which, as in the epidermic tissues in general, proceeds entirely from the pre-existing cells, unaided by free cell-development, of which there is in this case no indication. By endogenous development round portions of contents, or by division, cells are continually produced at the bottom of the glandular vesicles. These are at first pale, and contain but few granules, like the epithelial cells from which they arise; but as they are forced towards the interior by cells developed after them, they are very

soon completely filled with moderately large, round, dark, fat granules. They thus proceed towards the excretory ducts; and the fat drops contained in them running more and more together, and the membranes themselves becoming rather more resistant, they eventually assume the form of the sebaceous cells above described. The free fatty matter in the sebaceous secretion is formed, in certain cases, by the solution of the cells whilst still in the interior of the glandular vesicles, for, in fact, in many glands, free fat, in smaller or larger, often very considerable drops (fig. 86 *B*), is met with, even in the terminal vesicles; however, it is also, perhaps, produced in consequence of its draining from closed cells, a supposition which is not a little strengthened by the circumstance, that the fat-containing cells in the excreted sebaceous matter, are seldom filled to distension, but appear for the most part variously flattened, or even corrugated, and contain only a small quantity of fat. Understood in this way, the formation of the cutaneous sebaceous matter resembles in many respects that of the cuticle. The young, easily soluble cells at the bottom of the glandular follicles may be compared to the Malpighian cells of the *epidermis*, and the less soluble ones of the secretion filled with fat, to the horny plates, which seems the more appropriate, if we consider, 1, that the deep layer of the *epidermis* of the hair-sac is continued into the ducts of the glands, and even the outermost cells of the terminal vesicles; and 2, that the *epidermis*, in some situations being constantly detached, forms secretions (I refer to the *smegma præputii* of the *penis* and *clitoris*), substances which are, moreover, to all appearance chemically allied to the sebaceous secretion; for the latter, it may be remarked, according to an analysis of the contents of a distended gland by Esenbeck (Gmelin's 'Handbuch der Chemie,' Bd. II), contains principally, fat, 24·2; albumen and casein, 24·2; extractive matters, 24; and phosphate of lime, 20 per cent.; substances which are found, at all events in part, in the *smegma*.

Of *nerves*, I have seen no indication in the sebaceous glands, nor of *vessels* distributed upon and between their lobules; whilst numerous minute vessels and even capillaries, undoubtedly exist around the larger glands, most distinctly in the *penis* and *scrotum*, as well as in the ear. I would, moreover, refer to the *smooth muscles* described above, when speaking of the

cutis, which are found in the neighbourhood of the sebaceous glands, and whose contraction is, perhaps, not inoperative towards the emptying of their contents.

§ 75.

Development of the sebaceous Glands.—The first formation of the sebaceous glands takes place at the end of the fourth and in the fifth month, and is intimately connected with that of the hair-sacs, since they make their appearance simultaneously with the hairs, or shortly after, as *out-growths* of the *hair-sacs;* whence they are not all formed at once, but those of the eyebrows, forehead, &c., first, those of the extremities last. The mode of their development, more precisely described, is as follows:—When the rudiments of the hair-sacs have attained a considerable development, and the first indication of the hair is visible in them (fig. 75, *A, B*), there are perceptible, on their outer surface, small, indistinctly-bounded papillary processes (*u, v*), which consist of a cellular substance, solid throughout and continuous with the outer root-sheath, and of a delicate investment, which is continuous with that of the hair-sac. These processes of the external root-sheaths of the hair-sacs, as they may properly be called, at first of 0·02—0·03‴ length, and 0·01—0·016‴ thickness, now begin to grow in proportion to the hair-sacs, become globular, and finally, while they extend themselves and incline obliquely towards the bottom of the sac, pyriform and flask-shaped. A formation of fat in the internal cells now commences (fig. 88, *A*), which, beginning at the bottom of the pyriform processes, is continued, also, into their pedicles, and finally includes the cells of the outer root-sheath, until at last the fat-cells reach as far as the canal of the hair-sac (fig. 88, *B*). The gland and its contents are now complete, and it needs only that the cells at the bottom of the gland, or the glandular vesicles, should multiply, to force the sebaceous cells in the duct into the hair-sac, and fully to establish the secretion. The sebaceous glands, therefore, like the sudoriparous, are, at first, solid outgrowths of the Malpighian layer of the skin, for which an external opening is not developed till afterwards, and the first cutaneous sebaceous matter is formed by a metamorphosis of the inner cells of the rudiment of the gland, while the space which these cells occupied becomes

the cavity of the gland, which, however, never appears empty, but is continually filled by successive generations of cells.

The development of the glands, up to this point, proceeds pretty quickly. It may be stated generally, that so long as

Fig. 88.

the hairs have not appeared externally, the rudiments of the glands are papillary, measure scarcely more than 0·03‴, and for the most part contain cells which are still quite pale; after the hairs have made their appearance externally, we find larger pyriform rudiments with a thicker end, of 0·024—0·05‴, the cells of which are partly still pale, partly contain fat, and which now soon open into the hair-sac. In the fifth month, therefore, the secretion has already begun in many places, and in the sixth it is everywhere established. At the same time, however, it is to be observed that, together with the original glands, which occur, one or two together to each sac, in the sixth month, new rudiments are produced, which generally lie deeper, and taking on the same course as that which has been described,

Fig. 88. To elucidate the development of the sebaceous glands in a six-months' fœtus, × about 250: *a*, hair; *b*, inner root-sheath, here more closely resembling the horny layer of the epidermis; *c*, outer root-sheath; *d*, rudiments of the sebaceous glands. *A*, flask-shaped rudiment of the gland, with fat developed in the central cells; *B*, larger rudiments; the development of fat has taken place also in their neck, and fatty cells have been excreted into the hair-sac, giving rise to the glandular cavity and the secretion.

soon become secreting glands. The fatty cells of the newly-formed glands invariably contain many fat-globules, never a single large drop; nuclei also occur in them, as in the pale cells which surround them.

The further development of the sebaceous glands depends on the outgrowth of the external fatless cells of the originally simple tubular gland, into solid processes, which by degrees become changed into glandular vesicles, in the same way as the first rudiments. By repeated budding of the primitive or secondary glandular vesicles, the larger clusters are formed, and from them the most complicated forms which are met with. The so-called glandular rosettes proceed, very often, from a single rudiment, which, growing rapidly, surrounds the hair-sac on all sides; at other times, however, from two or more primary processes of the outer root-sheath. In the seven months' fœtus, most of the glands are simple pedunculated follicles of 0·04—0·06‴ in length, and 0·02—0·03‴ in breadth, which are appended, singly or in pairs, to the hair-sacs; in the ear alone, do four or five glands of the simplest kind surround a sac, and form rosettes of not more than 0·06‴ in diameter; in the nose, simple clusters of at most 0·1‴ are presented. In the new-born infant, instead of the simple follicles, simple *racemose-glands* are found in all the above-mentioned situations, one, or more rarely two, to a sac 0·1—0·12‴ in length, and only 0·04—0·06‴ in breadth; on the chest, the glands are rosette-like, also on the ear, temple, nose, nipple, *labia majora*, and *scrotum*, where they measure 0·1‴, in the last four places even 0·4‴ and more. From these data, it results, that after birth an increase in size takes place in most of the glands, and assuredly in the same manner as during the fœtal period, a view which is favoured by the occasional occurrence of pale solid glandular lobules, even in the adult; certain glands arise only after birth, viz. those of the *labia minora*.

[Sebaceous glands also occur in abnormal localities; thus Kohlrausch (Müll. 'Arch.,' 1843, p. 365), observed them in an ovarian cyst, and Von Bärensprung (l. c., p. 104) in a subcutaneous cystic tumour of the brow; in both places they were connected with hair-sacs, whence it may, perhaps, be concluded, that they are very frequently to be found in cysts which contain

hair. In fact, I met with very beautiful sebaceous glands, with a considerable amount of sebaceous matter, in the walls of the cyst containing hair, mentioned above, from the lung (Mohr's case); Von Bärensprung has, he believes, though rarely, observed a new development of sebaceous glands in cicatrices of some years' standing. When the hairs fall out, the sebaceous glands seem to disappear, at least I have repeatedly failed in finding them in bald places. Hypertrophy of the sebaceous glands takes place, according to E. H. Weber (Meckel's 'Archiv,' 1827, p. 207), in cutaneous cancer; according to Von Bärensprung in *akrothymion*, or moist warts (l. c., p. 81), and in *nævus pilosus*. The *comedones* also, among which I place *Lichen pilaris*, at least as Simon defines it (l. c., p. 334), are hair-sacs and sebaceous glands distended with sebaceous matter, which are especially frequent where the glands are distinguished by their large size, as on the nose, the lips, the chin, the ear, the *areola*, and the *scrotum*. They arise, either in consequence of the obstruction of the apertures of the hair-sacs by impurities, or of the formation of a more viscid and consistent secretion; and they contain, besides one or many hairs, which may also be wanting, fatty cells, like those of the normal cutaneous sebaceous matter, *epidermic* cells proceeding from the hair-sacs, free fat, often crystals of cholesterin and the *Acarus folliculorum*. *Milium* consists of small white spots on the eyelids, the root of the nose, the scrotum, and ear, which are formed, as Von Bärensprung is certainly right in supposing, from the sebaceous glands also, by their distension alone, without the hair-sacs; in consequence of which, rounded prominences without any aperture are formed and raise up the skin: their secretion, similar to that of the *comedones*, may still frequently be pressed out through the hair-sacs. Finally, there can no longer be any doubt that the sebaceous cysts which lie in the corium itself (*atheroma*, *steatoma*, *meliceris*, and *molluscum*), must also be regarded as colossal hair-sacs with sebaceous glands. Further details may be found in the works cited.

With respect to a little parasite, the *Acarus folliculorum*, which resides in healthy and distended hair-sacs and sebaceous glands, I must refer to G. Simon (l. c., p. 287). In the case of *Ichthyosis congenita* above referred to, Dr. H. Müller and I found the excretory ducts of the sebaceous glands in the

epidermis everywhere dilated to 0·02—0·06‴, with saccular diverticula, often lying many together one behind another, of 0·04—0·12‴, and quite full of sebaceous matter. Here and there a hair was found in one of these ducts, so that it appeared at the same time, to be a hair-sac.

In *investigating* the sebaceous glands, they should either be prepared from within, by cutting them with the hair-sacs which belong to them from the cutis, or perpendicular sections, not too fine, may be made. The minuter structure may be best studied, at first in the glands of the *scrotum* and *penis,* or *labia minora,* as these can be isolated without any trouble; to which end acetic acid, which renders the surrounding parts transparent, is very serviceable. With the others, so far as form, position, and size, are concerned, the use of alkalies, especially of caustic soda, is most advisable, inasmuch as they clear all the other parts, while they act but little on the glands on account of the quantity of fat they contain. If it be desired to study, not so much the investments, as the cells of the glands, obtaining at the same time a view of their whole figure, there is no plan better than maceration; the hairs with their root-sheaths, and the cellular masses of the sebaceous glands, *epithelium* and contents, may then be drawn out altogether. Where the epidermis is thin (on the *scrotum, labia majora, glans penis*), the same end may be attained in a short time by the dropping on it concentrated acetic acid, and also by using caustic soda in the same manner, though with greater destruction of the glandular cells. To study development, the maceration of fœtal skin, and the rendering it transparent by acetic acid, are of great use. The fat-cells in the interior of the glands are isolated with great ease by teasing out a large gland, and the secretion may be examined without addition, and also with water and caustic soda.

Literature.—Compare the works cited above under the head of 'Skin,' by Gurlt, p. 409; Krause, p. 126; G. Simon, p. 9; Valentin, p. 758; the 'Essay on the Hairs' by Eschricht, which has been mentioned; then the general works by Henle, p. 899; Todd and Bowman, p. 424, fig. 92; Hassall (pl. liv should be liii), p. 401; Bruns, p. 349; Gerber, p. 75, figs. 40, 42, 43, 44, 45, 239; Arnold, part II, the figures of Wagner, 'Icon. Phys.,' tab. xvi, fig. 11, *c*; Arnold, 'Icon. Anatom.,'

Fasc. II, tab. xi, fig. 10, and Berres, tab. xxiv, besides that G. Simon, 'Ueber die sogenannten Tyson'schen Drüsen an der Eichel des männlichen Gliedes,' in Müller's 'Archiv,' 1844, p. 1.

OF THE MUSCULAR SYSTEM.

§ 76.

To this system belong all the *transversely striped muscles*, which, together with their accessory appendages, the tendons and fasciæ, serve for the movements of the skeleton, of the proper organs of sense, and of the integuments. These muscles constitute a system situated between the integuments and the bones, and between the bones themselves, the individual parts of which are so associated and united by common membranes, that they may conveniently be regarded as a whole.

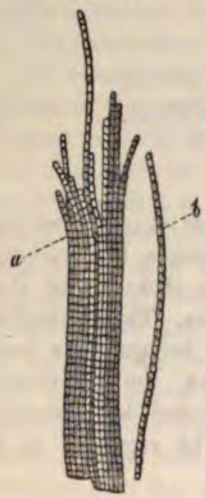
§ 77.

The proper *elements* of the muscles in question, visible even to the naked eye—the *transversely striated* (animal or voluntary) *muscular fibres*, or *primitive fasciculi*,—are distinguished, especially by their size and the distinctness of their individual parts, from those of most of the striped muscles occurring in other situations (heart, large venous trunks, *pharynx*, *œsophagus*, *larynx*, *urethra*). With respect to this latter characteristic, it is to be remarked that the sheath of the primitive fasciculus, or the *sarcolemma*,[1] in every fasciculus without exception,

[1] [It is greatly to be doubted whether the universality of the occurrence of this structure should be so strongly affirmed. We have been unable to detect it either in the muscular bundles of the heart, or in the great majority of those of the tongue, or in any of the muscles of a seven months' fœtus. In fact, the question of the existence of a sarcolemma as an independent structure, very much resembles that of the existence of "fibrils." The sarcolemma must be considered merely as the outer portion of the transparent, homogeneous matrix, in which the "sarcous elements" are imbedded (*vide infra*); and the possibility of raising it up by artificial means, or of observing its optical expression, as a distinct structure, will depend upon the amount to which it is developed relatively to the various elements—and the extent of chemical differentiation which has gone on it as compared with the rest of the matrix.—Eds.]

especially on the addition of water, acetic acid, and alkalies, may at once be recognised as a perfectly structureless, transparent, elastic, smooth membrane; which in man, as in the mammalia is distinguished by its delicacy from the same tissue in the lower Vertebrata, and particularly in the naked Amphibia. The *muscular* or *primitive* fibrils may, though not without difficulty, be isolated, especially in muscles that have undergone slight maceration, or have been boiled, or immersed in alcohol or chromic acid. In general they are varicose, that is to say, present more or less distinct enlargements, at intervals of 0·0004—0·001‴; in consequence of which arrangement, and owing to the circumstance that the thicker and thinner spaces, throughout the entire thickness of the *fasciculus*, are placed regularly on the same level, the latter for the most part appears to be marked with delicate *transverse bands*. Occasionally, moreover, in addition, a fine parallel striation is evident, or more rarely, where the enlargements on the fibrils are less apparent or quite imperceptible, simply a *longitudinal striation*. In adults, the fibrils do not enclose any central space or canal (Jacquemin, Skey, Valentin), but, with the addition of a small quantity of a connecting interstitial substance, constitute perfectly compact fasciculi (fig. 90). On the inner side of the *sarcolemma*, numerous *nuclei* always exist, of a lenticular or fusiform shape, frequently with *nucleoli*, and from 0·003—0·005‴ long. These *nuclei* are not placed with any regularity; sometimes two or more at the same level, or in rows, or alternately one behind the other. Fatty, or yellowish pigment-granules, also, frequently occur around the *nuclei* and between the fibrils, chiefly, however, in muscular fibres, which are not in a perfectly normal condition.

Fig. 89.



The form of the muscular fasciculi is rounded-polygonal. In thickness they vary from 0·005—0·03‴, or more; in the trunk

Fig. 89. Primitive fibrils from a primitive fasciculus of the Axolotl (*Siredon pisciformis*), × 600 diam.: *a*, a small fascicular composed of them; *b*, an isolated fibril.

and extremities, they are invariably thicker (0·016—0·03‴) than on the head, in which situation, especially in the facial

Fig. 90.

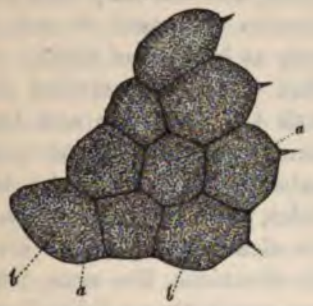


Fig. 91.

muscles, they are distinguished by the smallness of their fibres (0·005—0·016‴); but with respect to this, it is to be remarked that great differences not unfrequently exist in one and the same muscle. From all that is known, it would appear that there is no absolute difference in the size of the muscular fibre in man and in woman, or between weak and robust individuals. On the other hand, it is not improbable that in one case, one extreme, and in a second the other, may prevail. The thickness of the primitive fibrils, in man, amounts on the average to 0·0005‴; their number, in one of the larger fasciculi, must reach several hundreds, but is not accurately known. The distance between the transverse striæ varies usually from 0·0004‴ to 0·001‴.

[Various controversial opinions still prevail, with respect to the constitution of the muscular fibres. Several authors assert, or at all events consider it probable, that the primitive fibrils are produced artificially. This is the opinion entertained by Remak, who thinks a pre-existing division of the muscular cylinder still problematical; of Brücke, who appears to regard the contents of the muscle-tubes during life as fluid;

Fig. 90. Transverse section of some muscular fibres or primitive fasciculi from the *gastrocnemius* of man, × 300 diam.: *a*, sarcolemma and interstitial connective tissue; *b*, transverse section of the muscular fibrils, with the interstitial substance.

Fig. 91. Portion of a muscular fibre of man, treated with acetic acid, × 450 diam.: *a*, sarcolemma; *b*, simple nucleus; *c*, double nucleus, surrounded with fatty molecules.

of Du Bois-Reymond, and above all of Bowman. According to the latter, a division of the muscular fibres into "discs" (fig. 92) is quite as natural, although not so frequent, as that into fibrils, and that they may be considered as columns composed of such discs, quite as correctly as bundles of fibrils. Were a muscular fibre completely divided in the direction of both the transverse and longitudinal striæ, rounded, angular, minute particles would be produced, which may be termed primitive particles, or "sarcous elements." In the fibre, these elementary particles are connected in both directions, the same particles in the one case constituting a "disc," and in the other a segment or joint of the fibrils. The division into discs, upon which Bowman lays especial stress, would in my opinion have been of importance, had it occurred as frequently as that into fibrils, and also, occasionally, in recent muscle, but it is not so,—for in the first place, nothing of the sort can ever be seen in recent muscles of man and the higher animals; and in the second place, even in macerated, or otherwise manipulated fasciculi, the breaking up into discs is an extremely rare phenomenon; whilst on the other hand, the isolation and exhibition of the fibrils may be obtained, in almost every instance, by any one at all conversant with the subject. Moreover, in *transverse* sections of *perfectly fresh* living muscles, as for instance of the thigh of a Frog, made by means of the double-bladed knife, the transverse section of the fibrils is just as evident and distinct as in dried muscles, whilst, in precisely similar *longitudinal* sections, not a trace of the "discs" can be detected. This fact at once sets aside all those views, according to which the muscular fibres, during life, consist of a homogeneous, solid or fluid substance, or of minute particles, connected in two directions. To Bowman's opinion, moreover, is opposed the fact, that his assumed "elementary particles,"

Fig. 92.

Fig. 92. *A*, a primitive fasciculus, separating transversely into discs, × 350 diam. It exhibits distinct transverse and fainter longitudinal striæ. The discs, of which one more highly magnified is seen at *B*, are granular, and consist of the primitive particles (sarcous elements) of Bowman, or segments of the fibrils according to other authors (after Bowman).

except in macerated muscles, where such a thing readily occurs, can only with difficulty be obtained in an isolated form, whilst according to his view, such a disintegration, in cases where these particles do not cohere firmly, either in a longitudinal or transverse direction, would necessarily take place with equal facility in either; and in the second place, that in the thoracic muscles of Insects, the individual fibrils may be very distinctly and beautifully seen (fig. 93) in the muscles, when quite fresh. When we consider the great similarity between the muscles of insects and of the higher animals, in every essential particular, this fact appears to me to be of a striking nature. I am, therefore, from this and the other reasons assigned, thoroughly convinced of the existence of fibrils during life, and believe that, where they do not so readily admit of being isolated, as in man and many animals, they are connected by a homogeneous, tenacious (albuminous), interstitial substance, which is very evident in a transverse section, and in fact so firmly, that under certain circumstances, transverse rupture of the fasciculi may take place, that is to say, in the direction of the thinner spaces of the fibrils; as also occurs in other fibres; for instance, in the elastic tissue, smooth muscles, and even in the corneous cells (internal root-sheath and cortex of the hair). With all this, it must not be supposed that fibrils exist in all muscular fibres of animals, either themselves striped or corresponding to the striped fibres here described. The study of development and of comparative anatomy much rather teaches that the muscular fibre occurs in various conditions, and particularly, that it frequently exhibits more homogeneous contents, with or without transverse striation, and without fibrils. This however, of course, affords no ground for the assumption of such a condition in man and the mammalia also; and although such muscular fibres, in certain animals, readily break up into transverse segments (Leydig), still it is not thereby

Fig. 93.

Fig. 93. Primitive fibres from a quite recent transversely-striated muscle of a Bug, × 350 diam.

proved, that in the higher animals, a similar division of the contents is to be regarded as natural, and that into fibrils as artificially produced.

The diameter of the primitive fasciculi varies, not inconsiderably, in different muscles, or in one and the same muscle. Henle (who is followed by Gerlach), at an earlier period, assigned to them a diameter of 0·005—0·006‴, and at most of 0·017‴, but more lately (Stadelmann, "Sectiones transversæ"), has declared that these measurements are not universally correct. I will here give some particulars upon which the measurements stated above, in the text, are founded. In a female, the fasciculi of the *sacro-lumbalis* measured 0·016—0·028‴, the majority 0·020—0·022‴; in the *pectoralis major* 0·01—0·03‴, most of them 0·02‴; *deltoid* 0·016—0·026‴, the majority 0·02—0·022‴; in the *masseter* 0·006—0·02‴, the majority 0·01 — 0·018‴; in the *retrahens auriculæ* 0·006 0·015‴, the greater part 0·008—0·01‴. In a male, their diameter, in the *pectoralis,* amounted to 0·018—0·28‴, the greater number measuring 0·02—0·022‴; in the deltoid 0·012 —0·024‴ for the largest, and for the smaller 0·016—0·02‴; in the *obliquus abdominis externus* 0·16—0·024‴ and 0·016—0·02‴; in the *orbicularis oris* 0·008—0·016‴ and 0·01—0·012‴; in the *frontalis* 0·006—0·014‴ and 0·008—0·01‴. In a second individual, the *pectoralis major* contained fibres of 0·0068—0·024‴, most of them 0·018—0·02‴; the *pyramidalis,* some of 0·01—0·028‴, the majority 0·02‴.

With respect to the nature of the *primitive fibrils,* much still remains to be cleared up. In general they must be regarded as solid, and in fact there is nothing to indicate the existence of a cavity in them. It is fully ascertained, that it is to them, that the transverse striation of the primitive fasciculus is due. It is still doubtful, however, whence the appearance of transverse striation in the fibrils themselves arises; whether from their being *spirally twisted* (Arnold); from *zigzag curvatures* (Will); or from *varicosities.* All that I have seen, leads me to adopt the latter view, which is also that most generally entertained. I do not deny, that in the examination of numerous fibrils, appearances are occasionally met with, favorable to the other two views, and particularly to that of Will, but it is much more usual to find simple nodular

enlargements. The large fibrils in the perennibranchiate Amphibia (*Siren, Proteus, Menopoma*), (fig. 89), are above all others adapted for this investigation. In these animals, when they have been preserved in spirit, the fibrils become isolated in considerable numbers, and may be examined on all sides; it is the same with the muscles of the thorax in Insects.

Quite lately, Dr. Barry, has propounded the view that each muscular fibril is constituted of two spirally convoluted filaments running in the same direction. I have seen nothing of the kind, and do not hesitate to describe the whole of Dr. Barry's exposition as nothing but a myth, and his figures as fantastical images.

As regards the notion adopted by Bowman, Dobie, and others, that the fibrils are constituted of still more minute particles (sarcous elements), it may perhaps be stated, as the study of development shows, that the fibrils do, in fact, at first appear to consist of separate particles. But the question is, whether in the adult such elementary particles continue to be evident, and this, at present, I am inclined to deny.

The *nuclei* of the muscular fibres, in man, are situated, as I agree with Schwann in stating, only on the inner surface of the sarcolemma, and not within the fibrils; that they are not placed externally on the fasciculi, as was formerly stated by Henle and Stadelmann, and more lately by Gerlach, is readily perceived, when the muscles are treated with alkalies. Under these circumstances the partially-swollen nuclei escape, together with the fibrils, in a state of solution, from the sheaths, which remain behind, and before they are dissolved may be easily examined in an isolated state. In many muscles, even when there are no granules between the fibrils, larger or smaller fatty molecules occur around the nuclei.][1]

[1] [With regard to the vexed question of the ultimate structure of striped muscle, we question if any real improvements have been made upon the description originally given by Mr. Bowman ('Phil. Trans.,' 1840), viz. that it consists of minute, dark, subangular particles, the "sarcous elements," imbedded in a more transparent connecting substance or matrix; that neither discs nor fibrils can be said to exist in the normal state,—the breaking up of the muscular bundle into either of these elements, resulting simply from the manner in which the lines of greatest cohesion are disposed, at the time when mechanical violence is applied to it. The assertion in the text that the fresh muscle of Man and the Mammalia does not break up into discs, is decidedly erroneous—as we have seen it occur repeatedly.

Nor can we grant the invisibility of the discs in longitudinal sections of muscle:

§ 78.

The *muscular fibres* in the trunk and extremities are, in general, so associated, without the existence of any divisions,

what may be the case in such sections made with the double knife, we do not know, —but in those accidental longitudinal fractures of the muscular bundles of Man, Mammals, and Insects, which constantly occur, the edges of the discs are most distinct. Again, without making any section at all, the discs may, especially in Insects, be traced, by altering the focus of the microscope through the entire thickness of the bundles. The argument in the text, in fact, proves too much; for if the fibrils are visible over the whole transverse section, their dark parts (discs) alternating with the light ones, must be as visible in a section, made in any longitudinal plane, as they are on the surface. However, that the appearance of discs should be absent in any longitudinal section of striped muscle is, to us, simply incomprehensible.

With regard to the thoracic muscles of Insects, it is to be observed, in the first place, that they *do not represent ultimate fibrils*, but *non-fibrillated primitive bundles.* Dr. Auber, in a valuable paper in 'Siebold and Kölliker's Zeitschrift' (H. 3 and 4, 1853), has already shown that there is no defined line of demarcation to be drawn between these and the ordinary muscles of Insects, the two forms passing into one another by the peculiar flat bundles of the Libellulidæ, though he still considers the thoracic muscles to represent ultimate fibrils. His sole argument, however, is their resemblance to the ultimate fibrils of the higher animals, which we think loses all force, when we consider a fact that he has overlooked, namely, that the muscles of the legs, &c. present a very beautiful, though very delicate, fibrillation—the fibrils being not more than $\frac{1}{20000}$—$\frac{1}{30000}$th of an inch in diameter; that is, not more than from one third to one sixth the diameter of the thoracic muscles (fig. 93 *A*, 3, 4, 5). Examined carefully with a high power (600), with a good definition, the edges of the discs, which under a lower power appeared very sharp and even, are seen to be distinctly granular, and to be composed of minute, somewhat fusiform or rounded particles, not more than $\frac{1}{20000}$th of an inch in diameter, distinct from one another, and imbedded in the general transparent matrix, which is marked by fine longitudinal lines running between the rows of particles. Occasionally, the broad, dark discs appear to be separated by a delicate line; and this line, if carefully examined, is found to be composed of similar, but far more minute and paler particles (4, 5, 7). However, this appearance, though very common, is not to be met with in all the bundles. Acetic acid swells the muscle up, and renders the sarcous elements still more distinct, though the whole becomes very pale. If dilute ammonia be added to such a bundle, so as to neutralise the acid, it resumes its original dimensions, and almost its original appearance, except that the sarcous elements have often a wonderful sharpness of outline (93 *A*, 7).

The thoracic fibres, treated with acetic acid, become exceedingly pale, and the distance between the discs is much increased (93 *A*, 2). The latter often assume a granular appearance, but not so distinctly as in the former case; nor have we been able to detect any fibrillation of the intermediate substance, nor any minute sarcous elements, in them. They share the former character, however, no less than the latter, with multitudes of unquestionable muscular bundles—so that taking into con-

reticular connection, or termination in the interior of the muscles, as to constitute contiguous prismatic bundles extending

sideration the existence of fibrils very much minuter than the thoracic fibres, in the muscles of Insects, and the gradual transition of the latter into undoubted bundles, we do not hesitate to regard these thoracic fibres as homologous, not with primitive fibrils, but with primitive bundles; and therefore to neglect any argument which may be drawn from their existence, to that of primitive fibrils during life in the higher animals.

The answer to the question, whether primitive fibrils exist during life or not, in fact, depends very much upon the meaning of the words. If it be meant, that the muscular bundle is like a rope, the fibrils being the separate strands, united by "a homogeneous, tenacious substance,"—we should say that nothing of the kind exists during life. If, on the other hand, it be meant only that the molecules of the muscle are so arranged as to break up more readily and more frequently in the longitudinal direction than any other (just as a bar of wrought iron would tear into longitudinal fibres rather than in any other way, though it could by no means be said that it was composed of longitudinal fibres), why,

Fig. 93 *A.*

Fig. 93 *A.* 1, thoracic muscle of a Fly (*musca domestica*) unaltered, × 600, from an animal just killed: 2, similar fibre acted on by weak acetic acid, which distends the matrix and separates the discs, rendering the whole at the same time excessively pale: 3, a muscle of the leg, unaltered; the delicate fibrillation and the minute dark sarcous elements, arranged side by side to form the "discs," are well seen; *a*, nuclei in the centre of the bundle: 4, the edge of a similar bundle, showing a very common appearance—as if a row of minute sarcous elements were interposed between each pair of larger ones, and thus giving rise to the appearance of the fine dark line between the discs: 5, the same treated with acetic acid, and showing this appearance still more distinctly: 6, edge of a bundle treated with acetic acid, and exhibiting none of the minute sarcous elements: 7, a bundle treated first with acetic acid and subsequently with ammonia—sarcous elements very sharp and distinct: 8, 9, edges of bundles of facial muscles of the Rat; in 8 with the minute sarcous elements, in 9 without them: 10, 11, 12, from the Frog; 10, a fibril in the ordinary state; 12, a fibril greatly stretched; 11, edge of a bundle, showing the large and distinct sarcous elements, all of one size.

the entire length of the muscle. These *secondary muscular fasciculi,* as they are termed, are, each of them, enclosed by a

there can be no question that such is the fact. The behaviour of a muscular fasciculus, under the alternate action of acetic acid and ammonia, is as instructive with regard to this point, as that of bundles of connective tissue.

The existence of varicosities of the fibrils must depend very much upon their state of extension. Normally, they do not exist, unless, perhaps, the fibril has been split off from the very edge of a bundle, where the sarcous elements often project strongly (fig. 106 *A*, 4). When very much stretched again, since the sarcous elements are more solid and resisting than the matrix, they will form knots, and the fibrils will appear more or less varicose (fig. 93 *A*, 12). The great majority of instances in which the fibrils appear varicose, however, depend on imperfect definition—and the same may be said of supposed zigzag bendings; while the spiral fancies, on the other hand, are more probably connected with an imperfect judgment.

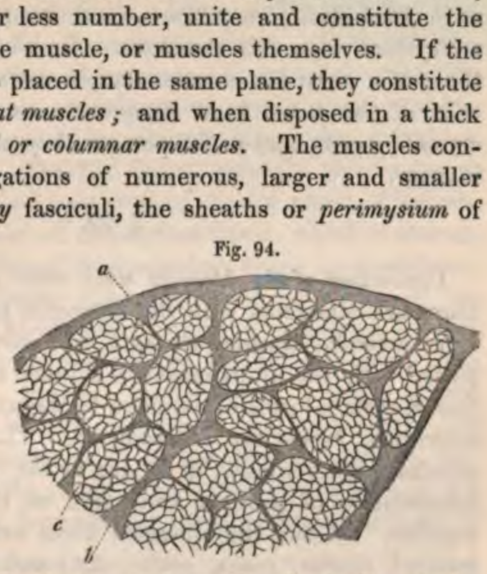
Recently, Drs. Sharpey ('Quain's Elements') and Carpenter ('Manual of Physiology') have advocated a view, the former, however, with some doubts (to which Professor Kölliker does not refer), founded upon an examination of the preparations of muscular fibrils, made by Mr. Lealand. They distinguish quadrilateral dark spaces in the fibrillæ, each of which is set, as it were, in a transparent frame of the same shape; these joined together constitute the fibril, the lines of junction of the frames, or "cells" being indicated by a dark line. We have repeatedly seen the appearances which are thus described; but so far as we have been able to discover, they invariably arise from that peculiar interposition of rows of minute paler sarcous elements, between the ordinary broad dark ones, to which we have referred above in describing the muscles of Insects. In fig. 93 *A*, 13, we have represented the edge of a bundle of fibrils from the heart of the Sheep, in which the structure described by Drs. Carpenter and Sharpey appeared very obvious at first sight,—but on close examination, the dark lines evidently proceeded from interposed rows of very minute sarcous elements. 8 represents the same appearance in the facial muscles of the Rat.

Very often, the finer sarcous elements are completely wanting, as in the thoracic muscles of Insects, in the muscles of the Frog (fig. 93 *A*, 10, 11, 12), and in many of the bundles in Mammals, as in 9, from the facial muscles of the Rat; and in these cases there is, of course, no evidence at all of the existence of any such "cells."

In conclusion, we may state the view which we are led to take of the structure of striped muscle, in a few words. In a homogeneous, transparent matrix, definite particles are imbedded—the sarcous elements,—which are arranged side by side, in even transverse rows. In some cases the sarcous elements are all of one size; in others, they are alternately larger and smaller. The reason of this difference does not at present appear, but it is very possibly connected with the nutrition of the muscle. The matrix usually tends to break up into longitudinal bands—the "fibrils,"—which have the diameter either of a single sarcous element, or of some multiple thereof; it likewise tends to break up in the transverse direction, giving way between the pairs of rows (discs) of sarcous elements; but these cleavage lines are no indication of the existence of discs or fibrils, as such, in the unaltered muscle. The sarcolemma is simply the outer portion of the matrix, and its demonstrability as a separate structure depends upon the extent to which it is developed, and the amount of chemical change which it may have undergone relatively to the inner portion.—Eds.]

special envelope of connective tissue, and, several together, united by stronger membranes into tertiary fasciculi, which, lastly, in a greater or less number, unite and constitute the separate bellies of the muscle, or muscles themselves. If the muscular fasciculi are placed in the same plane, they constitute the *membranous or flat muscles ;* and when disposed in a thick bundle, the *elongated or columnar muscles.* The muscles consequently are aggregations of numerous, larger and smaller *secondary* and *tertiary* fasciculi, the sheaths or *perimysium* of which constitute a connected system, in which that portion which surrounds the entire muscle, as the *perimysium externum* or muscular sheath (*vagina muscularis*), is to be distinguished from the more internal elements immediately surrounding the larger and smaller fasciculi and the muscular fibres—the *perimysium internum.* The thickness of the secondary fasciculi varies from $\frac{1}{6}$ to $\frac{1}{2}'''$; that of the tertiary and still larger bundles, which are most evident in muscles with coarse fibres (*glutæus maximus, deltoideus*), is so various, and the division of the muscle in these more remote constituents is so arbitrary, that there is nothing specially to be said with respect to them.

Fig. 94.



The muscular sheaths or envelopes, *perimysium*, composed of connective tissue, which are for the double purpose of conveying the vessels and nerves of the muscles, and of connecting the muscular fibres and supporting them when in action, vary in thickness according to the greater or less size of the groups of fasciculi surrounded by them. They are always, however, delicate, dull-white, non-glistening tunics, consisting of common connective tissue, and minute, isolated or anastomosing *elastic fibres*, of at most 0·001''' in thickness, the latter occurring in

Fig. 94. Transverse section from the *rectus capitis anticus major* of Man, × 350 diam.: *a*, external *perimysium ; b, perimysium internum ; c*, primitive fasciculus and secondary muscular fasciculus.

greater number, especially in the *perimysium externum*, which may, consequently, very properly and conveniently, be regarded as a semi-elastic membrane, and its function estimated in accordance with this structure. In all muscles, especially in those of a more lax construction, a certain number of adipose cells of the usual kind (frequently containing beautiful fat-crystals) occur, and in fat persons they are found quite in the interior.

§ 79.

Connection of the Muscles with other parts.—The muscular fibres are connected with the moveable parts, the bones, cartilages, articular capsules, the skin, &c., partly in a direct manner, partly with the intervention of fibrous elements, the tendons, *fasciæ*, certain forms of muscular ligaments and membranes (*lig. interossea, membranæ obturatoriæ*). Those muscles which are attached either wholly, or at one or the other end without the intervention of tendons, constitute on the whole the smaller number. Where the muscular fibres arise directly from bone (*obliqui, iliacus, psoas, glutæi*, &c.) and cartilage (*transversus abdominis*, diaphragm), or rest immediately upon those structures (*serrati, omohyoideus, sterno-hyoideus*, aural muscles), they never extend further than to the *periosteum* or *perichondrium*, terminating abruptly on those membranes, with the fibres of which they are not, in any way, continuous, nor do they come into immediate contact with the bone or cartilage. Where the muscles extend to the skin, they either expand immediately beneath, and without any connection with it, or radiate in it, in the form of larger or smaller divergent fasciculi (facial muscles); in which case they appear to be inserted, at all events occasionally, at once into the filamentary processes of connective tissue.[1] But the precise mode of connection of these tissues has not yet been ascertained.

[1] [The insertion of muscles without the intermediation of tendons, directly into the connective tissue of the skin and mucous membranes, is seen very beautifully in the tongue and in the facial muscles of Mammals. The former case has been well described by Dr. Salter (Todd's 'Cyclopædia,' article 'Tongue'); the latter may be examined with great ease in the *levator labii superioris* of the Rat (fig. 94 *A*). Here, the muscular bundles run in the subcutaneous connective tissue, keeping a pretty even diameter until they nearly reach their insertions. They then divide into

§ 80.

The *sinews, tendons*, are brilliant, white or yellowish structures, composed almost entirely of connective tissue. They are subdivided according to their figure into the rounded, *cord-like, true tendons*, and into *membranous aponeuroses* (*centrum tendineum, galea*, tendons of the abdominal muscles, *latissimus dorsi, cucullaris*, &c.) The two forms, either in their external configuration, or internal constitution, do not admit of definite distinction; they consist of connective tissue, which is characterised by the *parallelism* of its elementary fibres, its *consistence*, and its *poverty* in *elastic filaments*. The elements of the connective tissue, the *fibrillæ*, may be readily perceived, in fresh tendon, to be, as they are everywhere, extremely minute. In the cord-like tendons, they are slightly wavy in their course, all perfectly uniform in size, parallel to the long axis of the tendon, and in the recent state so closely approximated, that the demonstration of the existence of *primitive* fasciculi is not easy. Such fasciculi, however, do exist, having a breadth of

many branches, each of which, either tapers off to a conical extremity, or divides into a number of delicate pointed processes. In either case, the ends of the muscular fibre gradually or suddenly lose their striation, and pass directly into the irregular nucleated bands of the connective tissue. No sarcolemma can be demonstrated in the branched ends of the muscles, and the bands of the connective tissue are directly continuous with the matrix of the muscle; the change, from the one to the other, being evidenced merely by the appearance of the sarcous elements. Nothing can afford a more complete proof of the homology between the pseudo-fibrillated tissue of muscle and that of connective tissue, than what we find here.—Eds.]

Fig. 94 *A*.

Fig. 94 *A*. Branched muscular fibres from the upper lip of the Rat: *a*, epidermis and aperture of a sebaceous gland; *b*, muscular fasciculi dividing at their extremities, the ultimate divisions becoming continuous with the irregular, more or less stellate bands of the subcutaneous areolated connective tissue; *c*, "nuclei" of the latter.

0·006—0·008‴ and a rounded polygonal figure, as may be seen, especially in transverse sections of dried tendons, particularly on the addition of alkalies. But in the natural state, they are so firmly united that they cannot be isolated.

On the other hand, in true tendons, in the recent state, *secondary* and *tertiary* fasciculi are very evident (fig. 95). Delicate dissepiments, in fact, of loose connective tissue, penetrate the substance of the tendon, and by their mutual connection form a continuous system of parallel tubes, thus dividing the tendinous fibrils or primitive fasciculi into numerous larger or smaller groups. Secondary fasciculi, mostly of a polygonal, or perhaps rounded or elongated figure, and having a diameter of 0·03—0·06‴, may be very readily distinguished; and tertiary fasciculi, with polygonal contours, of 0·1—0·05‴ and more in diameter, and bounded by rather stronger dissepiments; there are, also, generally apparent, still larger subdivisions, composed of numerous tertiary fasciculi, and which being closely united in very various numbers and groups, by a common envelope of lax connective tissue, constitute the tendon itself. The *aponeuroses* are constituted either in the same way as the true tendons, and consist of several layers of parallel, secondary fasciculi, disposed contiguously in the same plane; or, more resemble the fibrous membranes, and present primary and secondary fasciculi decussating in two or more directions (abdominal muscles, diaphragm).

Fig. 95.

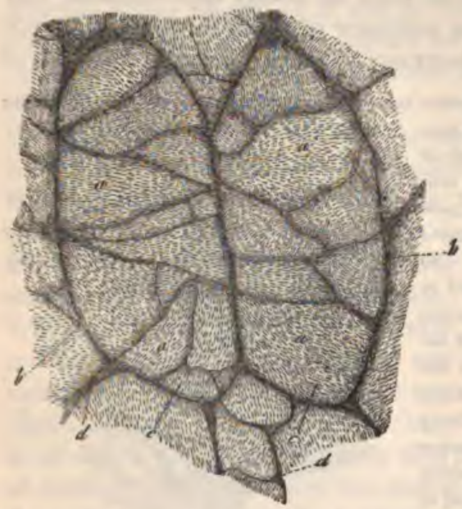
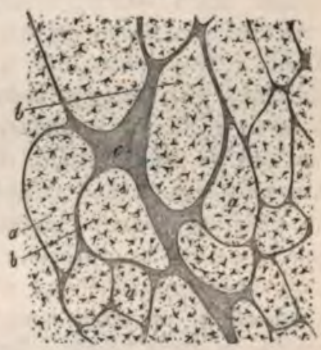


Fig. 95. Transverse section of a tendon of the calf, × 20 diam.: *a*, secondary fasciculus; *b*, tertiary; *c*, nuclear fibres not quite in transverse section, but appearing as little streaks in the former; *d*, interstitial connective tissue.

Fine elastic fibres (the so-termed nuclear fibres) occur in the secondary fasciculi of all tendons, in various conditions of development: sometimes as a series of slender fusiform cells connected by delicate processes; sometimes as fully-formed fibres of uniform thickness, or as isolated fusiform cells. The arrangement of these elastic elements is uniform throughout, and they run at regular distances, parallel to, and among the fasciculi of connective tissue. Consequently, in the transverse section of a tendon, the dark ends of the elastic fibres are apparent, distributed, at constant distances of 0·007—0·008‴ apart, over the whole section. But besides these stronger elastic filaments, measuring from 0·0005—0·001‴, there exist in most, perhaps in all tendons, extremely delicate fibrils of 0·0002—0·0004‴, connecting the former in various directions, so that in reality there is, in every tendon, an elastic network, penetrating and entwining the fasciculi of connective tissue. These fibrils may also be distinguished on a transverse section, as minute dark points, or as lines radiating from the coarser points exhibited in the section (fig. 96); and they are still more evident in longitudinal sections, in which more especially, the whole of the fibrous system just described comes very readily into view. In such sections, also, it is evident that, in every case, in which the formative cells of which the fibres are constituted still retain a certain degree of independence, very distinct elongated nuclei exist in them. Besides these elastic fibres, the tendons, in certain situations, contain cartilage-cells (*vid. infra*), as well as common *fat-cells*, particularly in the more lax tendons, as in the tendinous fibres of the intercostal muscles, of the *triangularis sterni*, *masseter*, &c.

Fig. 96.



The transversely banded aspect of the tendons, to which their glistening appearance is due, depends simply upon the numerous

Fig. 96. Tendon of the *tibialis posticus*, Man, × 60 diam.: *a*, secondary fasciculi; *b*, thicker nuclear fibres; *c*, interstitial connective tissue.

curves of their fibrils, which correspond with each other throughout the fasciculus; this appearance is destroyed when the tendon is forcibly stretched, and merely indicates its innate elasticity, which comes into play in the relaxed condition.

[The *primary tendinous fasciculi*, according to Donders and Moleschott, are seen in transverse sections treated with potass; this reagent, according to them, separates the secondary fasciculi into smaller ones, each of which consists of from 5 to 10 primitive fasciculi. In moistened transverse sections of dried tendon of man and the mammalia, I can very distinctly recognise the primitive fasciculi, although they have extremely delicate outlines. The appearance thus obtained affords an indistinct image of that presented in a transverse section of muscle. Even the very fibrils are, in this way, rendered distinct, a circumstance which appears to me of the greatest importance. When a *transverse*, not a longitudinal section of tendon moistened with water or acetic acid is examined, there will be observed in all the secondary fasciculi, or in the primary when they can be distinguished, if not in all, yet in most cases, an extremely regular and minute punctation, nearly like that of the muscular fasciculi (fig. 90), only not quite so distinct. The apparent granules are pale, round, of the same diameter as the tendinous fibrils which are obtained in other ways, and can be explained in no other manner than as being the transverse sections of such fibrils. These facts, better than any other, contradict Reichert's view, according to which, the tendinous tissue is composed of a homogeneous substance. (*Vid.* § 24, note).]

§ 81.

Connections of the Tendons with other parts.—The tendons are connected on the one side with the muscles, and on the other with the various parts moved by the muscles. Even by the naked eye, it may be seen, that the former connection is effected, in the one case, in such a way that the tendon and muscle are continued into each other rectilinearly, and in the other so that the muscular fibres, with rounded extremities, join the borders and surfaces of the tendons and aponeuroses at an acute

angle, as in the instance of the penniform muscles. The microscopic conditions in these two cases, are widely different. In the former, the muscular fasciculi pass immediately into those of the tendon, in such a way that no sharply defined limit exists between the two tissues, and the entire fasciculus of muscular fibrils is continuous with a nearly equal-sized bundle of tendinous fibrils (fig. 97). Extraordinary as it may sound, I must say,—in order to describe the impression that this sort of conjunction of muscle and tendon gives me,—that it is that of a continuous connection of the muscular and tendinous fibrils. Where the muscular fasciculi join the tendons and aponeuroses at an acute angle, we find,—in complete contrast with the condition just described,—an abrupt limit between the muscle and tendon (fig. 98). For in this case, the fibres of the muscle really end, for the most part, obliquely truncated, with a slightly conical projecting terminal surface, or, more rarely, perceptibly attenuated, though always rounded, and are attached at a more or less acute angle to the surfaces of the tendons and aponeuroses, and on the borders of the former. Notwithstanding this, however, the connection between the two tissues is of the most intimate kind. The extremities of the

Fig. 97.

Fig. 98.

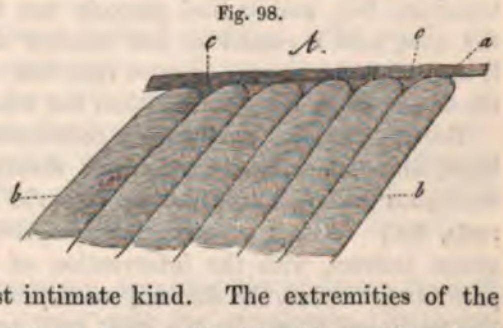


Fig. 97. A primitive fasciculus: *a*, from one of the internal intercostal muscles of Man, continuous into a tendinous fasciculus, *b*, into which it passes without any defined limit, × 350 diam.

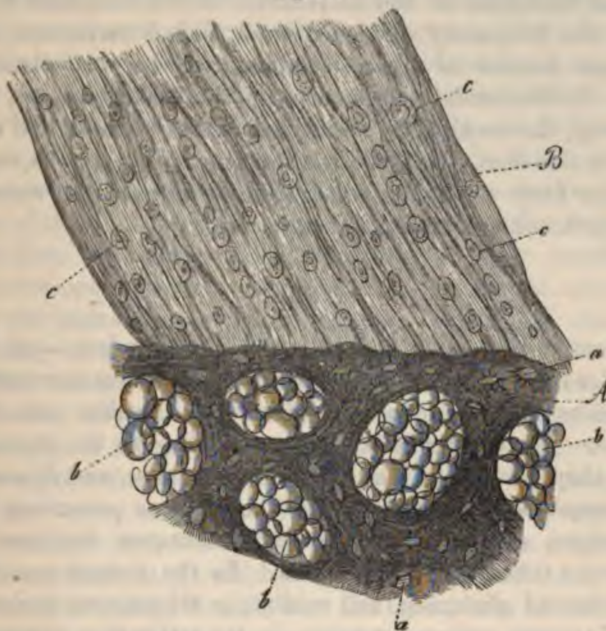
Fig. 98. Disposition of the muscular fibres, at their oblique insertion into the tendon of the *gastrocnemius* (Man), × 350 diam.: *a*, a portion of the tendon cut longitudinally; *b*, muscular fibres with slightly conical or truncated extremities, affixed in small depressions on the inner aspect of the tendon, to the border of which the *perimysium internum*, *c*, is connected.

primitive fasciculi are inserted into minute pits in the surface of the tendon, whilst, at the same time, the connective tissue between them, the *perimysium internum*, is continuous with that on the surface of the tendon. These relations are best observed in muscles which have lain a long time in spirit, or been boiled; in which also, the sacciform blind extremity of the sarcolemma may occasionally be clearly seen. The last-described condition occurs whenever muscular fibres and tendons meet obliquely, consequently in all semipenniform and penniform muscles; in those, whose tendons of insertion commence as membranous expansions (*soleus, gastrocnemius*, &c.), and which arise from the surfaces of fasciæ, bones, and cartilages. Where, on the other hand, aponeuroses or tendons, with their elementary tissues, join muscles in a straight line, a real transition, for the most part, takes place between the tendinous fasciculi and muscular fibres, but not always, for even in such apparently rectilinear transition of muscles into tendons, there is frequently an oblique insertion of the former, with free extremities, though at very acute angles; in such cases, for instance, as where tendons penetrate deeply into the substance of a muscle, and there divide into separate fasciculi. From what I have hitherto observed, there are many muscles, in which all the fasciculi connected with tendons begin or terminate free, and indeed scarcely one in which this is not the case, with a greater or less number of fasciculi; whence it may be deduced, as a general rule, that the tendons have for the most part a less diameter than the muscles.

Besides muscles, tendons are connected with bones, cartilages, fibrous membranes (*sclerotica*, sheath of the optic nerve, tendinous fasciæ), ligaments, and synovial membranes (*subcruralis*, &c.) With the first-named textures, the connection is either *indirect*, with the intervention of the *periosteum* and *perichondrium*, into the similarly constituted elements of which, the tendinous fibres, for the most part, are continuous, or to the thickness of which they appear to add, or direct. In the latter case (*tendo Achillis*, tendons of the *quadriceps, pectoralis major, deltoideus, latissimus dorsi, ilio-psoas, glutæi*, &c.) the tendinous fasciculi rest, at an acute or right angle, on the surface of the bones, and become attached, without the intervention of the periosteum, which is wholly wanting in these situations, to

all the elevations and depressions of the surface (fig. 99). Close to the bones, the tendons frequently contain, throughout

Fig. 99.



a certain extent, delicate, isolated cartilage cells, which are sometimes, however, contiguous and disposed in small rows. In exceptional cases, I have also seen the tendinous fibrils, at their extremities next the bone, entirely incrusted with calcareous salts, in the form of granules (ossified). In fibrous membranes, the tendons cease quite imperceptibly, and without any interruption of continuity (*tensor fasciæ, biceps humeri*).

[In man, I must positively deny that the tendinous fasciculi are ever connected merely with the sarcolemma (Reichert). Nor could I satisfy myself that this is the case in the River-crab, in which, the tendons, it may be remarked, consist of chitine. Whilst other animals have afforded indubitable evi-

Fig. 99. Insertion of the *tendo Achillis* into the calcaneum of a Man 60 years old, × 300 diam. *A*, bone with lacunæ, *a*; canalli and fat-cells, *b*: *B*, tendon with tendinous fibrils and cartilage cells, *c*.

dence of the existence of the same conditions as in man, the Frog, in particular, presents evidence of this fact; in the tadpole of which, owing to the sparing development of pigment in the tail, the transition of the extremities of the muscular fibres, which are frequently divided into 3 and 5 serrations, into the same number of minute tendons, may be very distinctly seen. In the caudal muscles also, of the Cod, I noticed, very distinctly, the continuous connection of the tendons and muscles; in this case, owing to the shortness of the muscles, many muscular fibres were even seen in their entire length, together with the tendinous fasciculi at each end.[1]]

§ 82.

Accessory organs of the Muscles and Tendons.—*A.* The muscular envelopes or *fasciæ* are fibrous membranes surrounding single muscles or entire groups of muscles, together with their tendons. They differ in structure according to the degree in which they partake of the character of *tendons* and *ligaments*, or of *simple muscular sheaths;* in the one case presenting that of tendons, and in the other of membranes composed of connective tissue and elastic fibres. In the former case they are white and glistening, and exhibit, in all respects, the structure of tendons and aponeuroses; in the latter they frequently

[1] [There can be no doubt that both the modes of connection between muscles and their tendons, described above, exist. Is it not possible, that the gradual transition or the sharp line of demarcation between the muscle and its tendon, may have some connection with the age and completeness of the particular bundle examined? In the Frog, we have noticed that among neighbouring bundles, some exhibit transitions between the proper muscular tissue and the tendon, while others have the former very sharply defined; and the examination of the insertion of the *triceps extensor cubiti* of a seven-months' fœtus has afforded us the most evident transitions from tendon into muscle, although the insertion of the bundles is here very oblique (fig. 106 *A*, 5). The best way of expressing the mode of connection of muscles with their tendons, perhaps, would be to say, that the matrix of the muscle and the matrix of the connective tissue, into which it is inserted (whether in the form of tendon or otherwise, are invariably continuous; the appearance of continuity or of discontinuity of the two tissues, arising solely from the sudden or gradual cessation of the deposit of the sarcous elements at their point of junction.

The nature of the corpuscles which are to be found at the junction of tendons with bones and cartilages—Professor Kölliker's "cartilage corpuscles,"—has been adverted to in the note at p. 81.—Eds.]

contain a larger quantity of fine elastic fibres in their connective tissue, and in some places may even assume the structure and dull-yellow aspect of the elastic membranes (*vid.* fig. 49), and contain a close elastic network of the strongest kind. The *fasciæ* are always of the tendinous character, where for some mechanical purpose a tough unyielding structure is requisite. They are of this kind, therefore : 1. At their origin from bones. 2. Where muscles arise from them; and they are of the nature of aponeuroses. 3. Where tendons radiate into them and they themselves act as terminal tendons. 4. Where thickened portions of them supply the place of ligaments. On the other hand they are more or less *elastic,* where they constitute a firm envelope to the muscles, but, at the same time, one which does not impede their changes in form. This is their character, especially in the middle of the limbs.

[The *membranæ interosseæ* (forearm, leg, *foramen ovale*), which are not usually reckoned among the fasciæ, are not apparently of the nature of ligaments of the bones, but rather of intermuscular ligaments. The plantar and palmar aponeuroses serve, in part, as tendons for the smaller muscles of the hand and foot, but chiefly as ligaments for the retention of the flexor-tendons, in which respect they are analogous to the *lig. cruciatum carpi dorsale,* &c. In them, even in the adult, the entire course of development of the nuclear fibres (minute elastic fibres), may be studied. Between the fasciculi of connective tissue, straight series of 10 to 20 and more, thickly placed, elliptical cells of 0·006 to 0·012‴, with round nuclei, and 2 to 6 minute opaque fat-granules, occasionally occur; the cells afterwards disappear, and the nuclei, which, on the addition of acetic acid, appear a little yellowish, become more and more elongated, and transformed into long, slender, straight, or slightly-curved fibres, which are, finally, conjoined into long nuclear fibres; these fibres, however, upon the whole are rare. The elongated nuclei are not always placed in a straight line, one behind the other, but frequently in an oblique, and in various other directions. In this way are produced serpentine nuclear fibres, which, even when fully formed, are still surrounded with isolated fat-granules, and lie as it were in vacant spaces in the connective tissue. In this case, consequently, the nuclear fibres are not formed from the nuclei of the cells, from

which the connective tissue is formed, but from special cells of a temporary nature; which circumstance, were the fact of general application, would make it intelligible, that nuclear fibres may both surround the secondary fasciculi of connective tissue, and also exist without any such tissue (membranous, reticular expansions of nuclear fibres, 'Mikr. Anat.,' II, 1, p. 226).]

B. Ligaments of the tendons.—The tendons are retained in their positions by various ligaments. Independently of certain ligamentous portions of the fasciæ, which, being attached to the bones, form tubular processes around tendons, or otherwise confine them, there are the so-called *tendinous sheaths* (*lig. vaginalia tendinum*), as for instance on the flexor tendons of the fingers and toes, where they are formed of numerous successive narrow bands, which in these situations serve to strengthen the mucous sheaths. Other ligaments to be referred to this class, are the *lig. carpi proprium*, the *trochlea*, and the *retinacula tendinum.*

C. Mucous bursæ and sheaths,—bursæ mucosæ et vaginæ synoviales.—Where muscles or tendons, in their movements, rub upon hard parts (bones, cartilages), or on other muscles, tendons, and ligaments, there are found, between the parts in question, spaces filled with a slightly viscid fluid, which, according to Virchow (Würzb. 'Verh.' II, 281), contain not mucus, but a material very similar to colloid matter, and which anatomists have been used to regard as lined with a special membrane, a *synovial membrane.* These spaces are said to constitute closed sacs of a rounded or elongated form, which either simply invest the opposed surfaces of bones and tendons, bones and muscles, &c.,—*bursæ mucosæ;* or in the form of double, although connected tubes, cover at the same time the surface of the tendons, and of the parts between which the tendons play,—*vaginæ synoviales.* The truth of the matter is this, that it is only the smallest of these spaces which are lined with a continuous membrane; most of them are in many situations without such a lining. With respect to the mucous *bursæ,* those appertaining to the muscles (*psoas, iliacus, deltoid,* &c.), are, eminently, to be considered as continuous sacculi, whilst in those belonging to the tendons, a membrane can only be detached in parts, and is found to be almost wholly wanting exactly at the points where the mutually gliding parts are in contact. Precisely the same thing obtains in the synovial

sheaths, among which the common sheaths of the flexor tendons of the fingers and toes, only in a certain measure, retain the form of a so-termed serous sac, although, even in this case, many parts of the surface of the tendons are without any such membranous lining. Whence it would appear, that in this case, as in many others, the old doctrine of the existence of continuous serous sacs requires thorough emendation. In most of the synovial sheaths, and in many mucous bursæ, are found occasionally, particularly in the *retinacula*, smaller or larger, reddish, fimbriated processes, exactly resembling those of the joints, and which, in like manner, are nothing but *vascular processes* of the synovial membrane.

D. Fibro-cartilages and *sesamoid bones*.—The tendons of some muscles (*tibialis posticus, peronæus longus*), in those portions which run in the tendinous sheaths, contain, imbedded in their substance, dense, semi-cartilaginous bodies, which are known under the name of *sesamoid cartilages* (*fibro-cartilagines sesamoideæ*), and when, as occasionally happens, they become ossified, of sesamoid bones (*ossa sesamoidea*); the latter occur normally, imbedded in the flexor tendons of the fingers and toes, presenting one surface towards an articulation.

Respecting the more intimate structure of the last-mentioned parts, the following is to be remarked. The sesamoid bones consist of common, finely cancellated osseous substance, are on one side closely surrounded by tendinous or ligamentous tissue, and on the other, which is invested with a thin layer of cartilaginous substance, project into an articulation. The *ligaments* of tendons, in correspondence with their function, possess exactly the same firm structure as that of the tendinous portions of the *fasciæ* and of the tendons themselves, and exhibit occasionally fine elastic fibres in process of development, or the round formative cells of such fibres disposed in rows. The *retinacula tendinum* have a more delicate structure; their function being rather to convey vessels to the tendons, they consequently contain chiefly a more lax connective tissue, with fine elastic fibres, and also fat-cells. The mucous bursæ, which are invariably thin-walled, consist, in as far as they possess a distinct membrane, of fasciculi of connective tissue, crossing each other in the most various directions, loosely connected, and in many places anastomosing, together with

some fine elastic fibres. The mucous sheaths, on the other hand, in agreement with their double function, which in one respect is that of a mucous bursa, and in another that of ligaments confining the tendon or of tendinous sheaths, present in their thinner parts the structure of *bursæ mucosæ,* and in the thicker, an unmixed, dense connective tissue, frequently with cells disposed in rows, which pass into elastic fibres. Both of these kinds of sacs are lined, on the inner surface, together with the parts contained in or otherwise bounding them, but only in places, with an epithelium, consisting for the most part of a simple layer of nucleated polygonal cells 0·004—0·007‴ in diameter. The parts which are bare of epithelium are:—many portions of the mucous sheaths, and the tendons lying in them, and certain spots of the *bursæ mucosæ* themselves, which are distinguishable by their dull lustre and yellowish aspect, and which occur especially in those situations where the tendons and parts surrounding them are exposed to a greater degree of pressure. The common flexor sheath of the fingers is lined throughout with epithelium; and the same may be said of the mucous bursæ, in which it is only certain loop-like ligaments, which beyond the limits of the bursæ still surround the tendons, that do not present any cellular covering, as is the case, occasionally, in the *subscapularis, poplitæus,* &c.

All these bare places, which are uncovered by epithelium, invariably exhibit, almost throughout, the nature of *fibro-cartilages,* the dense connective tissue of which they are composed, and which for the most part is furnished with but few elastic elements, containing a greater or less, often a very considerable number of cartilage-cells (fig. 99), amongst which, the most frequent are rounded cells, with a dark contour, although by no means with thick walls, measuring 0·006—0·012‴, with a roundish nucleus of 0·003‴, and clear fluid, with or without some minute, opaque, fatty granules. Besides these, there are, moreover, elongated cells, with one or two nuclei; round, thin-walled cells, containing 1, 2—20 secondary cells, with

Fig. 100.

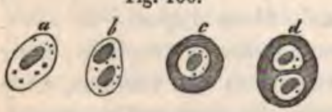


Fig. 100. Cartilage-cells from the vaginal ligaments surrounding the tendons of the *poplitæus*, × 350 diam.: *a*, cell with one; *b*, with two nuclei; *c*, cell with one; *d*, with two secondary cells, both of which have rather thick contents.

thick walls, and dark contours; the mother cells measuring as much as 0·02—0·03‴; and lastly, elongated cells with concentric deposits, inclosing a nucleus, or nucleated secondary cell. In the tendons, the simpler forms of cells almost exclusively occur, and the cells, although frequently extremely numerous, are for the most part isolated, or, at most, disposed in rows or groups of 2—6, which are contained in the connective tissue, both superficially and more deeply. In most cases the common connective tissue alternates with one more resembling fibro-cartilage, so that the tendon, on a transverse section, presents a speckled, white and yellowish aspect; or it may be, that the outer surface only of the tendon contains cartilage, the deeper portions retaining their usual condition. Where the deposition of the cartilage cells is most abundant, the tendons become thickened, or even studded, as it were, with distinct, fibro-cartilaginous masses (*peroneus longus, tib. posticus*). In the mucous bursæ and the other parts above named, the cartilage cells are placed, not unfrequently, in closer aggregation, or in longer rows of 5—10 cells or more, in which rows the terminal cells are invariably the smallest, and the middle ones the largest. On the cuboid bone, where the tendon of the *peroneus longus* passes over it, there is a layer of *true cartilage* $\frac{1}{3}$—$\frac{1}{2}$‴ thick.

The vascular processes of the tendinous sheaths and mucous bursæ, correspond with those of the articulations, only that they are for the most part of smaller size.

[The synovial-sacs of the muscular system are not mere meshes of connective tissue, like the subcutaneous mucous bursæ, since they have, invariably, an epithelial lining in certain places; they bear just as little resemblance, however, to the proper serous sacs (*pleura, peritonæum*, &c.), because, with few exceptions, their epithelium is never complete, and also because the cellular coat of the serous membrane is, almost universally, wanting entirely in some spots. The synovial sacs of the muscular system, on the other hand, and the synovial capsules, which also never possess a complete epithelium, and frequently communicate with mucous bursæ, (*quadriceps femoris, popliteus, subscapularis*, &c.) belong to one and the same category, and differ in some points from the serous sacs; with respect to

which, however, it must not be forgotten that transitionary forms between these two kinds of sacs exist.

No one seems to have remarked upon the occurrence of cartilage cells in the various textures which go to the construction of the synovial sacs of the muscular system (except in the fibro-cartilages of the tendons); and the more so, because even Henle refers the fibro-cartilage of the tendinous sheaths to his interarticular cartilages (bandscheiben). It is quite true that the cartilage cells, while often occurring isolated in the connective tissue, or more frequently only in certain spots aggregated together, are not always readily seen; they may, however, be recognised in sufficiently thin sections, and very distinctly on the addition of acetic acid. The cell-membranes are not in this case utterly destroyed, any more than they are in the cartilage cells of the interarticular ligaments, &c., and no doubt can be entertained as to their being true cartilage cells, which, almost without exception, exist, not as a tissue, but rather dispersed in the connective tissue. Those spots in which they exist in great quantity may be described as fibro-cartilaginous places; but the distinction between these fibro-cartilages and those with true fibres, not of the nature of cellular tissue (*epiglottis*, ossifying bones), must not be lost sight of. Genuine cartilage, as on the cuboid bone, I have never as yet met with in any other tendinous sheath; not even in the *sulcus malleoli externi et interni;* in the sulcus of the heel; nor in the sheath of the *peronæus longus* on the *calcaneum;* in which situations, cartilage cells are, indeed, everywhere to be seen, but only scattered in the connective tissue.

With respect to the rows of cells which are met with in ligaments of the tendons, and in the tendinous sheaths, the nuclei of which, after the disappearance of the cell, continue to grow and arrange themselves together in the form of nuclear-fibres, I cannot avoid remarking upon their close resemblance to the more simple cartilage cells of the tendinous sheaths and tendons, a resemblance so close, that I should almost be inclined to indicate it as marking their identity, if it did not sound altogether strange, to speak of a transition of the nuclei of cartilage-cells into nuclear fibres. If not as identical, still they may be regarded as analogous formations; and the rather

so, because in almost every case where cartilage cells occur in the connective tissue, rows of cells of this kind, and their relation to elastic fibres may be shown to exist, as well as in the interarticular cartilages, or ligamentous discs of Henle, as they are termed, afterwards to be described. On the other hand, it is true, similar rows of cells are to be found in the palmar fascia, tendons and ligaments, although those structures possess no indubitable cartilage-cells.]

§ 83.

Vessels of the Muscles and their accessory Organs. A. Blood-vessels.—The ramifications of the larger vessels present little that is peculiar. The trunks reach the muscles in an oblique or transverse direction and then subdivide, running in the *perimysium internum*, in an arborescent manner, and at acute or obtuse angles, so that every part of the muscle is supplied by them. The minutest arteries and veins usually run parallel with the muscular fibres, between which they constitute a vascular plexus, so characteristic that, once seen, it can never be mistaken. The interstices of the plexus are rectangular, with the longer sides parallel to the longitudinal axis of the muscle, and it is of course composed of two sets of vessels, one longitudinal, which, as is shown most conclusively in transverse sections of injected muscle, lie in the fissures between two muscular fasciculi, or in the irregular spaces left between several of them, and the other transverse, which, anastomosing in various ways with the former, surround the muscular fibres. Thus each separate primitive fasciculus is

Fig. 101.

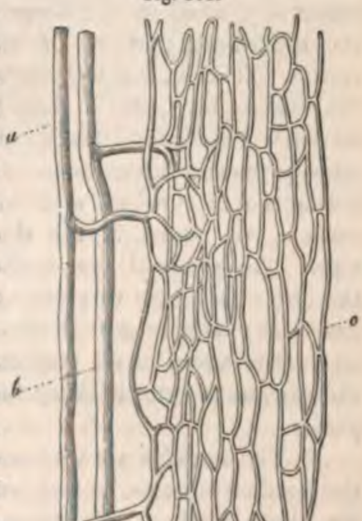


Fig. 101. Capillary vessels in muscle, × 350 diam.: *a*, artery; *b*, vein; *c*, capillary plexus.

lodged, to a certain extent, in a plexus of capillaries, and being surrounded on all sides by them, is very abundantly supplied with blood. The capillaries of muscle are among the most minute in the human body, their diameter being often less than that of the blood-corpuscles themselves. In one of Hyrtl's preparations, they measure 0·0025—0·003‴; in the *pectoralis major*, when filled with blood, 0·002—0·003‴, and when empty 0·0016—0·0020‴.

The tendons may be reckoned amongst those parts of the body which are the most scantily supplied with blood-vessels. The smaller tendons, in the interior, present no trace of vessels, whilst externally, in the more lax connective tissue by which they are surrounded, there exists a wide-meshed capillary plexus. In the larger tendons, a few vessels occur in the superficial layers, and in the largest, by means of the microscope and injection, a scanty vascular network may also be rendered evident in the deeper layers; but even in this case the innermost portions of the tendon are entirely without vessels. The tendon-ligaments present the same conditions as the tendons, only, that in them even still fewervessels can be perceived. The thinner fasciæ, also, are altogether non-vascular; sparing ramifications, exclusive of those in the lax connective tissue, amply supplied with blood-vessels, which covers their surface, are found in the thicker fasciæ, such as the *fascia lata*. The synovial membranes of the muscular system, on the other hand, are very vascular, and especially their vascular processes; with respect to these synovial membranes, however, since they agree in all respects with the synovial capsules of the osseous system, nothing further need be remarked in this place.

B. The muscles are very scantily supplied with lymphatics; the smaller muscles, in fact, such as the omohyoid, subcrural, &c., have none at all, either in their substance or on the surface; and among the largest muscles, it is only in some, that solitary lymphatics, measuring $\frac{1}{4}$ and $\frac{1}{5}$‴ are seen accompanying the blood-vessels. The deep or muscular blood-vessels in the extremities, it is true, are accompanied by lymphatics, but these are few in number; and from the latter two circumstances, it may be concluded, that even the larger muscles are but poorly supplied with these vessels. If they had

not actually been observed in the fasciculi in certain cases, it might have been a question, whether muscles in general did possess lymphatics at all; the occurrence of the deep lymphatic vessels proves nothing towards this, it being quite possible that the contents of these vessels, scanty as they are, might be derived from the skin (*vola manus, planta pedis*, &c.), from the joints, or perhaps from the bones. It may also be concluded, that if a few lymphatics really exist in the larger muscles, they do not run among the secondary fasciculi, but only in the more vascular *perimysium* between the larger and more lax subdivisions, and especially where the latter contains adipose tissue, and is consequently soft, as, for instance, in the *glutæus*, and in the superficial layers of the muscles.

Lymphatic vessels have never yet been noticed in tendons, fasciæ, and the synovial capsules of the muscular system. At the same time, it cannot be said, at all events in the latter instance, that lymphatics may not, as in other serous membranes, be contained in the sub-serous connective tissue.

§ 84.

Nerves of Muscles.—The distribution of the muscular nerves, with respect even to their coarser relations, presents considerable peculiarity, it being evident, in most muscles, that the nerves come in contact with their fibres only at a few limited points, and are by no means connected with them throughout their entire length. With respect to the *ultimate termination* of the nerves, it may be stated, that in all muscles there exist anastomoses of the smaller branches, forming the so termed "plexuses." These anastomoses among the larger branches are seen chiefly, if not altogether, where the entire ramification of the nerves takes place within an extremely limited compass (*vid.* note); elsewhere they rarely occur, or are wholly absent. Those between the smaller and smallest branches (*terminal plexuses* Valentin), on the other hand, are very numerous everywhere, forming elongated roundish meshes, which run for the most part parallel with the longitudinal direction of the fasciculi. These terminal plexuses, composed, sometimes of smaller, sometimes of larger meshes, and formed principally by the ramules of one small branch, though not altogether isolated one from the other, proceed to form what are termed by Valentin the *terminal*

loops; by which I understand nothing more than anastomoses of the ultimate twigs, effected by means of one or a few primitive fibres passing from one twig into another. It is consequently unimportant whether they follow a straight course, or are curved in a looplike form (fig. 102). Whether, besides these loops,

Fig. 102.

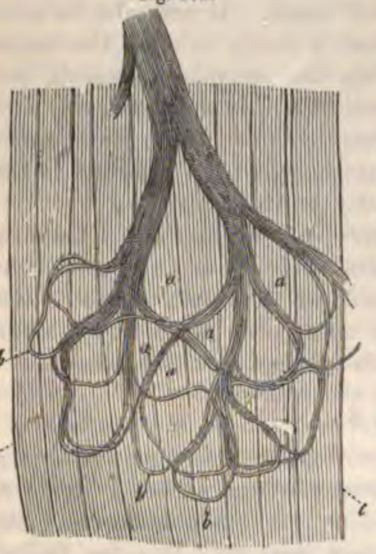


Fig. 103.

there are also, free terminations of the nerve-fibres, such as are known to exist in the lower animals, and as I believe I once noticed in a Rabbit, is altogether doubtful; whilst it is certain, that, even in man, divisions of the nerve-fibres take place, although they are rare, and detected with difficulty, and their relation to the loops, it must be confessed, is still to be made out.

The trunks entering the muscles are composed principally of thick nerve-fibres, about twelve of the finer ones occurring, on an average, among 100 of the larger (Volkmann). They become smaller in the interior of the muscle, so that the

Fig. 102. Ultimate expansion of the nerves in the omohyoid muscle of Man, × 350 diam., and treated with soda: *a*, interstices of the terminal plexus; *b*, terminal loops; *c*, muscular fibres.

Fig. 103. Divisions of the primitive nerve-fibres in muscle, × 350 diam. *A*, double division from the omohyoid muscle in Man; *a*, neurilemma: *B*, division of a nerve from a facial muscle of the Rabbit, into three apparently pointed twigs.

terminal plexus consists only of extremely minute fibrils, measuring 000·1—0·0025‴ in diameter. In some cases even, the gradual attenuation of the fibres may be directly observed, proving that the diminution in size does not take place, in this case at least, in consequence of division. Thus, in the omohyoid, I have noticed several nerve-fibres of 0·004—0·0053‴, derived from trunks measuring 0·05—0·07‴, become attenuated, within a distance of 0·15—0·2‴, to a diameter of 0·002—0·0026‴, and after a further course of 0·4—0·5‴, acquire that of the smallest fibrils, or 0·001‴. Simultaneously with this change in size, the nerve-fibres assumed in all respects the aspect of the so-termed sympathetic nerves, and ultimately became pale, with a simple contour line, and disposed to form varicosities; at the same time, that they appeared to lose every vestige of a coat composed of connective tissue, they still retained dark borders, and consequently were not non-medullated fibres (or free axis-cylinders), such as are seen in other terminations of nerves.

Nervi vasorum (vascular nerves), accompanying the bundles of vessels, occur in all muscles, and, according to the size of the latter, form larger or smaller branches. They are composed only of the smallest fibres, and always follow the course of the large vessels, which can still be recognised as arteries and veins. I have not seen how they terminate—and this much only I know—that they are never met with on the capillaries, and very frequently, also, are not to be found, on the smallest arteries and veins. Occasionally, one or more fibrils from the terminal plexus of the muscular nerves may be seen to join these vessels; a circumstance quite in accordance with the demonstrable fact, that the vascular nerves in many parts, for instance in the extremities, are derived from the spinal nerves.

The smaller *tendons* contain no nerves, and the larger, such as the *tendo Achillis* and the tendon of the *quadriceps femoris*, only vascular nerves. The *fasciæ* and *sheaths of tendons* are also without nerves, as well as the *synovial capsules* of the muscular system, so far as I am at present aware.

[In many of the small muscles, the extent of space included in the distribution of the nerve is extremely limited, as for

instance in the superior belly of the omohyoid, in a portion of which, three inches long, the space over which the nerves are distributed, does not exceed from five to eight lines in length. The trunk of the nerve entering in the middle of the transverse axis, divides into two equal primary branches, one passing towards the left, and the other towards the right border of the muscle, and each giving rise to numerous anastomosing branches of all sizes, and thus supplying the entire thickness of the muscle from the most superficial to the deepest layers. Whilst this distribution of the nerve takes place at one point,—a distribution not unlike that in an organ of sense,—the rest of the muscle presents the utmost poverty, or even a complete deficiency of nerves. In one case, which I examined closely, I was unable, besides the few vascular nerves in these portions, to detect more than three small nervous twigs of 0·021‴, 0·028‴, 0·042‴, which, though derived from the main nerves, differed from the other branches in their distribution. Two of them ran directly towards the lower, and one towards the upper end of the belly of the muscle, giving off a few filaments composed of one or two primitive fibrils which passed through the muscle, and terminated, a little before reaching the intermediate and terminal tendons, in the most minute twigs and single nerve fibrils. I found the same conditions of the nerves in the *subcruralis*, and in one of the costo-cervical muscles (arising from the first rib in the cervical fascia), as in the omohyoid; in the sternohyoid, sternothyroid, omohyoid (inferior belly), the same condition in some parts was noticed, whilst in others, one apparently different, existed, that is to say, the branches of the nerves frequently did not all divide at the same level, but were more widely spread. It was easily seen, however, that the above-described mode of division essentially obtained, also, in this case, viz. that the *separate portions of the muscles are in connection with the nervous plexuses, only at a point of limited extent.* The proof of the existence of similar conditions in other small muscles was more difficult, as in those of the orbit, where the nerves reach the muscles at acute angles, follow a longer course in them, with their primary branches, and form their ultimate ramifications at various, more or less widely separated points; yet even in this case it was tolerably well made out. It is

easy to understand that in the larger muscles, a microscopic examination, *in toto*, is impossible; but it can be shown in other ways, as by the preparation and examination of minute flat fasciculi taken in their entire length, that conditions exist, at all events in some of them, similar to those which appear to be evidenced in the small muscles. It is thus seen, especially in muscles of lax structure, that each fasciculus presents precisely the same conditions as an entire smaller muscle. How the distribution of the nerves is effected in muscles with long fasciculi (*sartorius, latissimus dorsi*, &c.), I have not examined; it is probable, that in this case, each primitive fasciculus is joined by the nerves at several points, widely apart.

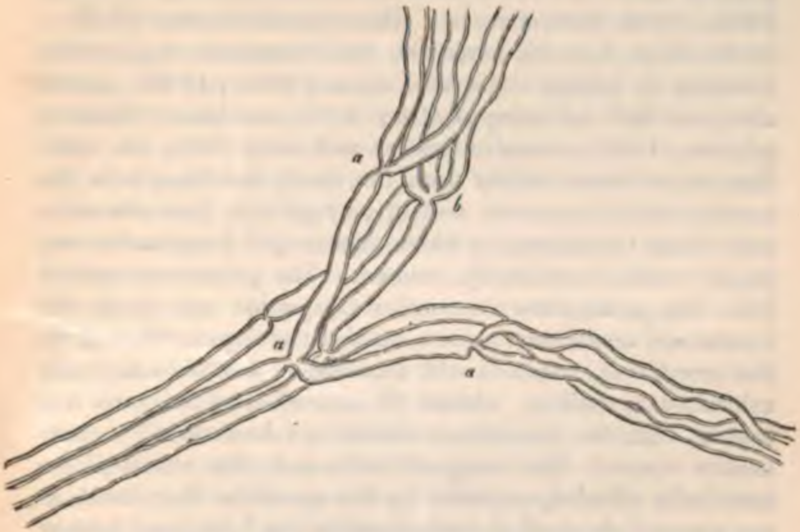
Valentin and Emmert, in the year 1836, simultaneously described the terminations of the primitive nerve-fibres in the muscles, to be in the form of loops, and the former maintained that the nerves of sensation terminated in a similar way. But Physiology having more recently shown that she does not well know what is to be done with these loops, and Microscopic Anatomy having distinctly demonstrated the existence, in many situations, of other modes of termination of the nerves (Pacinian bodies, &c.), the loops have fallen into such discredit, that the question now is, not as before, whether, besides the loops, there are other modes of termination, but rather, whether loops really exist anywhere? With respect to the muscles especially, anatomists seem inclined to deny their existence altogether, since divisions and terminations of nerve-fibres have been discovered in them; but this conclusion, from what has been remarked above, would be incorrect. Henle also, in Canstatt's Jahresb. f. 1847, p. 63, says, that in his opinion the loops had been too rashly discarded; while on the other hand, Wagner, with reference to this question, places the analogy with what is seen in the Frog, &c. above direct observation, and denies the existence of loops. With respect to divisions of the nerves, Wagner ('Gött. Nach.,' 1852, p. 27), finds them to be tolerably frequent in the muscles of the Mouse. I would, moreover, remark, that in one case, I think I noticed a minute ganglion with about five cells on a nervous twig in the omohyoid of man; the observation, however, was not satisfactory, the muscle having been previously treated with soda.

In the Invertebrata, many observers have long since de-

scribed free terminations of the nerve fibrils, and their insertion with expanded ends into the muscular fibres, as Doyère in the *Tardigrada,* and Quatrefages in *Eolidina,* and some Rotifera ('Ann. d. Sc. N.,' 1843, p. 300, and pl. 11, fig. 12). I myself, in a larva of *Chironomus* (a dipterous insect), noticed a single nerve-fibre, proceeding to the two muscular fasciculi of the simple tarsus, bifurcate into two branches, which were implanted upon the surface of the muscle, with somewhat expanded terminations. In the Vertebrata, Müller and Brücke first described division of the nerves in the orbital muscles of the Pike (J. Müller, 'Physiol.,' 4th ed. vol. 1, p. 524), and in *Amphioxus,* Quatrefages noticed conditions precisely like those met with in the Invertebrata above mentioned. The observation is easily confirmed, as respects the orbital muscles of the Pike, in which, upon the teasing out of the fasciculus either of the fresh muscle as well as after it has been treated with corrosive sublimate, and rendered transparent by acetic acid, numerous divisions of the nerves are apparent. They are nevertheless not nearly so frequent in this case, as in the Frog, nor are the divisions more than bifid or trifid. Besides this, I was especially struck with the glaring contrast that was presented, to what is seen in the Mammalia, in the enormous extent of space included in the distribution of the nerve-fibres; a distribution so extensive, that it is by no means easy to find a single primitive fasciculus which has not a nerve-fibre going to it; in many places even, the latter were seen in apposition with a fasciculus throughout a great extent, and surrounding it with loops, or with a variable number of spiral convolutions. A similar condition was observed by R. Wagner in the orbital muscles of the *Torpedo,* whilst in other muscles the nerves were very scantily supplied (' Gött. Nach.,' Oct. 1851). In the Amphibia, divisions and free terminations of the nerves have been described by Wagner. The former are remarkably beautiful and numerous. They commence in nerve-fibres, measuring 0·004—0·006‴, in the smaller trunks and branches, and are several times repeated, with a gradual diminution of the fibres, until extremely minute filaments measuring 0·001—0·0015‴ are formed. The divisions are for the most part di- or trichotomous, more rarely multiple; in one instance, however, Wagner noticed eight ramusculi. The ultimate filaments are

pale, and have a simple contour line. They never penetrate into the muscular fasciculus, but, after running a short distance, are

Fig. 104.



either applied obliquely or transversely to it, or proceed for some distance in close contiguity and parallel with it; in either case, becoming attenuated to a sharp point, and frequently as fine as a fibril of connective tissue. All these conditions are best seen in the *mylohyoideus* (Wagner), and above all, in a delicate cutaneous muscle of the thorax, as was pointed out to me by Ecker, and in which the distribution of the nerves has recently been very accurately described by Reichert. He observed in this case, as I had done in man, that only a small portion of the muscle was well supplied with nerves, which were but sparingly distributed to the other portions. The trunk of the nerve supplying the 160—180 fasciculi of this muscle, contains, according to Reichert, 7—10 fibres, and ultimately, by continual division, forms 290—340 terminal filaments, so that there is more than one for each muscular fasciculus.

Fig. 104. Divisions of nerve-fibres, in a small twig from the cutaneous thoracic muscle of the Frog, × 350 diam.: *a*, bifurcation; *b*, threefold division.

§ 85.

Chemical and physical Relations of the Muscles.—In 100 parts of fresh beef there are contained, according to Bibra, 72·56—74·45 parts of water. The solid constituents (25·55—27·44) in a man 59 years old, were composed of a residue insoluble in boiling water, alcohol, and æther, 16·83; soluble albumen and colouring matter, 1·75; substance affording gelatine, 1·92; extractive matter and salts, 2·80; fat, 4·24. The fat is derived chiefly from the blood, the fat-cells in the muscles and their nerves, and in part perhaps from the muscular fibres themselves, in which microscopic fat granules are, at all events occasionally, evident. The gelatine is derived from the *perimysium*, in smaller proportion also from the vessels and *neurilemma;* none, on the contrary, is afforded by the *sarcolemma*, which is still apparent in muscles completely exhausted by boiling, whence (in opposition to Reichert) it is evident that the *sarcolemma* should not be referred to connective tissue. The inorganic salts and the albumen are principally afforded, probably by the muscular fibre itself, as are also and above all the salts described by Liebig and Scherer in the juice of muscles, of the lactic, acetic, butyric, and formic acids, the free lactic acid, the creatin and creatinin, the sugar of muscles or inosit, and the colouring matter, which substances, even the last-named, are lodged partly in the fibrils themselves, partly and chiefly, and this is the case especially with the albumen, in the interstitial substance, by which the fibrils are connected together. The 16·83 parts of insoluble residue belong in part to the elastic tissue in the vessels and *perimysium*, and to the smooth muscle in the vessels, but principally to the muscular fibrils themselves, which, as we have before seen (§ 27), consist of a substance allied to fibrin. The *sarcolemma* is less affected by alkalies and acids than the fibrils, and approaches in its nature more nearly to the *membrana propria* of the glands, the walls of the capillaries, and the membrane of many cells. The colouring matter of the muscles (and the muscles themselves), like the blood, becomes bright red in the air, or still more in oxygen gas, and is rendered dark by sulphuretted hydrogen. It is extracted, and indeed readily, by water, but not by salts, in which circumstance, that

is to say, in an alteration in the degree of concentration of the plasma with which the muscle is imbued, is perhaps to be sought the principal reason for the readiness with which the colour of the muscles is altered in disease.

The muscles, although softer and more easily torn than the tendons, possess, nevertheless, considerable tenacity, particularly during life, and they have a certain degree of *elasticity*. During life, as has been correctly remarked by E. Weber, even when not under the influence of the nerves, they are not for the most part in their natural form, but stretched, or in a state of tension, and like harp strings in the same condition, exert an elastic force. This is satisfactorily shown when the tendons of the extensor muscles in an animal's limb which is strongly flexed, are cut through, the nerves having been previously divided, whereupon the tendons are very considerably retracted (E. Weber). This tension of the muscles varies very much, according to the position of the limbs. It is very slight when the body is at rest with the limbs semiflexed, still less or even wholly absent when a muscle falls into a state of repose after it has acted powerfully upon the limb; greater, and manifested in the greatest degree, when the antagonists of a muscle are acting with all their force. According to Weber, the living muscle, when in a state of inactivity, may be compared with caoutchouc, seeing that, like that substance, they possess a very great elastic extensibility; or, in other words, a *slight* but *very perfect* elasticity, as may be readily perceived in the muscles even of dead animals, which may be alternately stretched and allowed to retract. Owing to their elasticity, the muscles offer scarcely any hindrance to the movements of the limbs, and in consequence of its perfect nature, they recover their previous form and length even after the greatest possible extension. This is exemplified in the stretching of the abdominal muscles in pregnancy and in certain pathological conditions. When the muscles are in a state of activity, their elasticity alters in a very remarkable manner: 1. During their contraction they become more extensible or less elastic, on which account they exert a much less force by their contraction than would otherwise be the case, had their elasticity remained unchanged, and the same as in the inactive condition. 2. The elasticity of the active muscle,

in one and the same muscle, is extremely variable; it continues to diminish as long as it is in action, whence arise the phenomena of fatigue and loss of power in the muscles (E. Weber).

In the dead muscle, according to the same observer, the elasticity is less *perfect;* that is to say, the dead muscle, when stretched, does not altogether resume its pristine form, and consequently is more readily torn, although such a muscle as the *gracilis* may still be capable of supporting a weight of eighty pounds without breaking. But at the same time it is also less extensible, more rigid, less flexible,—or its elasticity is *greater.* The phenomena of fatigue in the muscles are consequently to be distinguished from those induced by death. In the former state, the diminution of elasticity occurs during the influence of the nerves and the contractions of the muscle itself, probably in consequence of changed conditions in the molecular nutrition of the muscle, and is consequently a vital phenomenon; whilst in the latter case, innervation, nutrition, and contraction have ceased, and the increase of elasticity, which produces what is termed the *rigor mortis,* is a purely physical phenomenon, and not to be confounded with the increased tension, which, under the influence of life, takes place during the contraction of the muscles, simultaneously with a diminution of the elasticity.

The *tendons* are very firm, and but slightly elastic; and contain, according to Chevreuil, in 100 parts, only 62·03 of water, considerably less therefore than the muscles. They consist principally of a substance affording gelatin, although they are transformed with more difficulty than other parts into that principle.

[In my opinion the muscles are sometimes in a state of tension, sometimes in their natural form, sometimes even compressed, and to all these three conditions vital contraction may be superadded. If a muscle in a state of extension contract, so as not to assume its natural form, it will still be in a state of tension after the remission of the contraction, and if divided will retract. On the other hand, if a muscle in its natural form contract, it will, after the cessation of the nervous influence, immediately become extended; as, for instance, the

contracted heart, or an isolated muscle excited by galvanism. Consequently, when we speak of the elasticity of muscles, their tension, not only when they are extended, but also in the compressed condition, must be considered; and this appears to me of some physiological importance, as in this way the extension of contracted muscles (heart), and of muscles whose antagonists are paralysed, becomes intelligible. With respect to the cadaveric rigidity, the important facts have quite recently come to light, that it may be arrested by the injection of blood (Brown-Séquard); and also that it takes place even in the living animal, when the supply of blood to a group of muscles is entirely cut off (Stannius). In the latter case, the irritability of the nerves ceases at the same time, and on the restoration of the circulation the normal conditions in both muscles and nerves are also restored. By these facts, all hypotheses respecting the occurrence of the cadaveric rigidity, except that of Weber, are contradicted; even that of Brücke, which asserts that it is caused by the coagulation of the fibrin existing in the muscular fibre. But at the same time the question also arises, as to what is the proximate cause of the change in the elastic conditions of the muscles, whether it be due to the death or cessation of activity of the nerves, or to the deficient supply of blood to the muscles themselves? Stannius decides in favour of the former supposition, and is consequently driven to the conclusion, that during life the motor nerves act upon the muscles, by reducing, during the state of repose, their natural amount of elasticity, whilst in the contraction of the muscle the influence of the nerves is momentarily relaxed. Thus, according to Stannius, the rigidity connected with contraction, and vital contraction, would be identical, and nothing more than the condition of the muscle when freed from all nervous influence, and lasting until the nerve again puts the muscle into a state of rest, or its substance is decomposed. I must own that in this view, which moreover had already been proposed by Engel ('Zeitsch. der Wiener,' Aerzte, 1849), I do not at present agree; and in particular would remark, that the circumstance of the contractions which occur during life being much more considerable than those which attend the *rigor mortis*, appears to be opposed to it.]

§ 86.

Development of the Muscles and Tendons.—The rudiments of the muscles consist, originally, of the same formative cells as those of which the rest of the body of the embryo is constituted; and it is not till afterwards that the muscles, tendons, &c., are gradually developed by a histological differentiation. In man, the muscles are not evident before the end of the second month; at first, however, they cannot be detected by the unaided eye; they are soft, pale, gelatinous, and not to be distinguished from their tendons. In the tenth and twelfth week they are more distinct, especially in specimens preserved in alcohol; and at this time the tendons also may be distinguished as somewhat clearer, but at the same time transparent streaks.

In the fourth month, both the muscles and tendons are still more distinct, the former being, on the trunk of a light reddish colour, the latter less transparent, and greyish, both retaining a soft consistence. From this period, both textures acquire more and more of the configuration which they afterwards retain, so that at the maturity of the embryo, —excepting that the muscles are still softer and paler, and the tendons more vascular and less white,—they no longer present any difference worth notice.

With respect to their intimate conditions, the primitive fasciculi, in the embryo, at the end of the second month, present the aspect of elongated bands (fig. 105) 0·001‴ to 0·002‴ broad, with nodular enlargements at different points, at which places are situated elongated nuclei; the bands exhibit either a homogeneous or finely-granular aspect, and but rarely an extremely faint indication of transverse striation. In their further development, these primitive muscular fasciculi, which, as comparative histology teaches, originate in cells arranged in a linear series, continue to increase in breadth and length, and their contents, the original cell-contents, are developed into the muscular fibrils. In the fourth month (fig. 106) they measure for the most part 0·0028—0·005‴, some even 0·006‴, whilst others do not exceed 0·0016‴ and 0·002‴. The larger ones are, still, always flattened, but of uniform width, and also considerably thicker than before, mostly with evident longi-

tudinal and transverse striæ, and even with fibrils, which admit of being isolated. It is partially evident, even in a longitudinal view, but still better in a transverse section, that in many cases, the fibrils do not occupy the entire thickness of the primitive tube, but that they are deposited around its *periphery*, the interior being as yet filled with a homogeneous substance as at first, and which now appears like a *canal* within the fibrils. All the primitive tubules possess a sarcolemma (*b*), which on the application of acetic acid or soda, appears as a very delicate membrane, which by the imbibition of water, may occasionally be raised from the fibrils. The tubes, moreover, as at first, present nuclei lying close upon the sarcolemma, and which frequently cause rounded elevations on the surface of the tube, and may be observed actively engaged in the process of multiplication. They are all vesicular, roundish, or elongated, with very distinct, simple or double nucleoli measuring 0·0004—0·0008‴, and frequently with two secondary cells in the interior. They are much more numerous than previously, and most frequently disposed in pairs closely approximated; but often, also in groups of three

Fig. 105.

Fig. 106.

Fig. 105. Primitive fasciculi of an eight to nine weeks' human embryo, × 350 diam.: 1, two fibres without transverse striæ; 2, fibres presenting the first indications of transverse striation; *a*, nuclei.

Fig. 106. Primitive fibres of a four-months' human embryo, × 350 diam.: 1, a fasciculus, with a clear, as yet, non-fibrillated substance in the interior: 2, fasciculus without such contents, with an indication of transverse striation; *a*, nuclei; *b*, sarcolemma.

or four or even six, either contiguous or arranged serially. From this period to that of birth, no further important change takes place in the muscular fasciculi, except an increase in their size. In the new-born infant they measure 0·0056—0·0063‴, are solid, rounded, polygonal, longitudinally or transversely striated, according to circumstances, as in the adult, with very readily isolated fibrils, and no longer any appearance of nuclei.

From what has been remarked, it is clear, that the *sarcolemma* represents the sum of the membranes of the coalesced cells, and that the nuclei of the youngest fasciculi are the original cell-nuclei, whose descendants are represented in the nuclei of the older fibres, which have multiplied by an endogenous process. The muscular fibrils are the altered contents of the original tubes, become solid; they appear, demonstrably in many instances, to be formed on the inner surface of the sarcolemma, from without to within, but in other cases probably in the whole of the tube at once.

The growth of the entire muscle is chiefly to be referred to the increase, both longitudinal and in thickness, of the primitive fasciculi; and the rudiments of all the future primitive fasciculi appear to be formed, probably even as early as the original rudiments of the muscle itself—in every case at the middle period of fœtal life. In the embryo, at the fourth or fifth month, they are perhaps five times as thick as in one at two months; in the new-born infant they measure for the most part twice, occasionally even three and four times as much as in the fourth and fifth month, and in the adult their size is perhaps five times greater than in the new-born child. The number of fibrils must necessarily increase in proportion to the size of the fasciculus, because, according to Harting, they are but little thicker in the adult than in the fœtus. The *perimysium* is developed, as I find in agreement with Valentin and Schwann, after the type of the common connective tissue, from fusiform, coalesced formative cells.

The elementary parts of the tendons are, in no case, formed earlier than those of the muscles; for, in embryos from the eighth to the ninth week, I have never been able to detect a trace of them, although at this time the muscular fibres are quite distinct. It is not till the third or fourth month, when,

moreover, they become distinctly visible to the naked eye, that their elementary constituents can be made out, at this time presenting the appearance of long parallel bands with elongated nuclei, which, as the observations of Schwann and myself (§ 24) on very young animals show, are formed by the coalescence of fusiform cells. As early as the fourth month they may be distinctly recognised as primitive fasciculi, which are wavy, and present, at intervals, elongated nuclei 0·0035—0·006‴ long, and 0·0016‴ broad, but are as yet without distinct fibrils, and not more than 0·0012—0·0016‴ wide. From this period up to the end of fœtal life, the fasciculi gradually increase in width, so that in the new-born infant they measure 0·002—0·0025‴; at the same time their fibrils are developed, as are also fine elastic filaments among the fasciculi, from special fusiform formative cells (*vide* § 23). If these fasciculi be compared with those of the adult, measuring 0·006—0·008‴, it is obvious, that the fasciculi of the tendons are continually acquiring an increase in thickness from their first origin, so that their proportional sizes in the four months' fœtus, the new-born child, and the adult, are about as 1 : 1, 8 : 6; and, also, that in every case the growth of the tendons must in a great measure be referred to the increased thickness and elongation of their fasciculi. It would, moreover, appear, that subsequent to the primary rudiments of the tendons, new fasciculi continue to be added during fœtal life.

Fig. 107.

[Some controversial opinions are still entertained with respect to the development of the muscular fibres. Reichert and Holst maintain that each fibril is the product of a single cell, and regard it as the equivalent of the smooth muscular fibre, or contractile fibre-cell. This view is erroneous, as is readily shown by the examination of the mammalian and human embryo. Leydig's declaration, quite recently, in its

Fig. 107. From the *tendo Achillis* of a new-born child, × 250 diam., treated with acetic acid, in order to show the formation of fine elastic fibres.

favour (Beitr., p. 78), is explained by his having confounded the peculiar *secondary* muscular fasciculi in the plagiostomous fishes with the *primitive* fasciculi of the higher Vertebrata. In the Batrachia, according to Lebert and Remak, in the development of the muscles, elongated *simple cells*, with self-multiplying nuclei, are found, the contents of which cells undergo a metamorphosis similar to that occurring in the elongated muscular tubules formed of numerous cells, which, according to my observations, also exist in these animals. The contractile part of the muscular fibre, whether it be transversely striped or not, and whether it present fibrils or not, is generally developed from without to within, in the sarcolemma, forming a sort of tube which does not become solid till afterwards; less frequently it appears as a more solid cord on one side within the muscular fibre. In the former case, the nuclei and the original contents of the formative cells, which often contain a large quantity of fatty matter, are situated in the interior of the embryonic muscular tubule, or between it and the sarcolemma; in the latter always close upon the sarcolemma.

With respect to the pathological relations of these tissues, the following remarks may be offered:—The substance of the striated muscles is not regenerated, and wounds of muscles heal simply with a tendinous callus. A new formation of them has been noticed by Rokitansky ('Zeitsch. der Wiener,' Aerzte, 1849, p. 331), in a case of tumour of the testis in an individual 18 years old, and by Virchow ('Verh. d. Würzb.' Ges. I.) in an ovarian tumour. In the latter case, which came under my own observation, there were elongated, fusiform, transversely striated cells, each with a nucleus, similar to those described by Remak in the Tadpole. The state of the elementary parts in *hypertrophy* of the muscles is uncertain. This condition, however, except in the tongue, heart, and certain respiratory muscles (Bardeleben), does not perhaps occur at all; it is at all events extremely rare in the striped muscles. (Romberg, 'Nervenkr.,' p. 291, asserts, that such a condition ensues upon long-continued cramps, though it appears to me that this point is not yet sufficiently established.) Equally uncertain, also, is the intimate condition of the muscular elements in the increased development caused by exercise, and

whether this depend upon the growth of the pre-existing muscular fasciculi, or on the introduction of new ones—the latter of which suppositions may perhaps be affirmed without much chance of error, in the case of the extreme degrees of pathological hypertrophy. *Atrophy* of the muscles is very frequent, as in old age, paralysis, particularly of the tongue, and in cases of lead-poisoning, and in the development of cancer, fibrous tumours (consequent on inflammation), and of fat, &c. in the substance of the muscles. The processes, however, which are set up in these cases, have as yet been but little investigated. In extreme old age I find the fasciculi small, presenting occasionally a diameter of not more than 0·004—0·008‴, easily broken up, mostly without transverse stripes, and with the fibrils indistinct, whilst they frequently contain yellowish or brown granules, as much as 0·001‴ in size, often in large quantity, and very many vesicular nuclei with nucleoli. The nuclei often form continuous rows, or are accumulated on the inner surface of the sarcolemma, exhibiting in a peculiar manner the same distinct indications of an energetic multiplication by endogenous formation, as are presented in the embryo (*vide this* §, *supra*). In *fatty degeneration*, the muscular fasciculi are, by degrees, replaced by connective tissue and fat cells which are developed between them; whilst, at the same time, minute fatty molecules are developed in great number within them, in place of the fibrils, which gradually disappear.

Paralysed muscles were found by Reid ('On the relation between Muscular Contractility and the Nervous System,' 'Edinburgh Monthly Journal of Med.,' 1841) to be thinner, softer, and paler; and Valentin ('Phys.,' 2 ed. 2 Th., p. 62), noticed in such cases that the transverse stripes were indistinct, or had disappeared, and could no longer be produced by water, alcohol, &c.; the longitudinal stripes existed, but did not present their usual aspect, more resembling those of macerated muscle. Subsequently the altered fasciculi disappeared in part, and were to some extent replaced by fat. In a case of atrophy of the *pectoralis major* caused by cancer, I noticed conditions similar to those I had observed in old age, viz.: destruction of the fibrils, the development of brownish granules, and the presence of numerous nuclei, together with a clear fluid

in the persistent sarcolemma; and lastly a diminution of the fasciculi, which did not measure more than 0·002—0·004‴ in width. I also believe, that I noticed in many fasciculi the development of larger, serially disposed cells, with very large and distinct nuclei, exactly like the so-termed cancer-cells. The condition of the muscles in emaciation is unknown. In an emaciated Frog, which had fasted for eight months, Donders observed that the fasciculi were more slender, which he attributed chiefly to the removal of the interstitial substance between the fibrils. *Paleness* of the muscles is very common in dropsy, chlorosis, paralysis, lead-poisoning, old age, &c.; in which cases, probably, the numerous brown or yellow granules are formed from a portion of the colouring matter. This condition is generally associated with *softening*, in which the fasciculi no longer exhibit any distinct transverse striæ or fibrils, and readily break up into numerous particles, or even into a pultaceous matter. In *tetanus*, in which rupture of a muscle frequently occurs, Bowman ('Phil. Transact.,' 1841, p. 69) observed on the fasciculi numerous nodular enlargements, in which the transverse striæ were very closely approximated, and between them either actual rupture of the fibrils, or at all events a considerable stretching and disorganization of them, both of which states are clearly to be referred to a powerful and irregular contraction. The muscles sometimes contain *concretions*, particularly as the result of the cretification of pus, tubercles, and *cysticercus*-vesicles; sometimes also true bones, such as are produced after prolonged exercise in the deltoid and other muscles (Exercirknochen). Of *parasites* are to be noticed the not unfrequent *Cysticercus cellulosæ* and *Trichina spiralis*; and, besides these, in the Eel a nematoid worm, observed by Bowman ('Cyclop. of Anat.' II, p. 512) alive, in the almost empty sarcolemma. I met with something analogous to the latter, some years ago, in the abdominal muscles of the Rat (as have V. Siebold and Miescher also in the Mouse); that is to say, white streaks 4—7‴ long, and 0·09—0·01 wide, which, on microscopic examination, proved to be hollow primitive fasciculi, entirely filled with elliptical, slightly curved corpuscles, 0·004—0·005‴ long by 0·0019‴ wide, and manifestly ova. The portions of the fasciculi thus transformed into pouches, had walls, 0·009—0·01‴ thick, with transverse stripes, and

were continuous at either end with the perfectly normal fibre.[1]

[1] [We are unable to agree altogether, either with the statement of the facts of the development of muscle, or with the interpretation of them offered by Professor Kölliker. In the first place, we have been quite unable to discover a sarcolemma in the fœtal muscular fibres, even at the seventh month; on the other hand, the edges of the discs formed quite sharp projections (fig. 107 *A*, 1,4). Even where, as in the case of fig. 2, there was an appearance of a sarcolemma, it could readily be shown to arise merely from the stretching of the transparent matrix; and that it did not proceed from any defined membranous investment.

Fig. 107 *A*.

According to Professor Kölliker, again, the sarcolemma is formed by the united cell-membranes; the proper muscular substance by the contents of the original cells. At fig. 4 we have represented such "fusiform muscle-cells," from the triceps of a seven-months' fœtus, near its insertion into the tendon; fig. 5 showing the transition of the two tissues into one another. At *a a*, are the "nuclei," sometimes inclosed in distinct cavities. Now we wish to draw particular attention to these points, viz. that the "nuclei" of the muscle correspond exactly with those of connective tissue, and therefore with the corpuscles of cartilage (see note, § 24); and, furthermore, that the proper muscular substance and the sarcolemma are directly continuous with the pseudo-fibrillated portion of the connective tissue, the one corresponding to its collagenous, the other to its elastic element. It necessarily follows then, (according to what has been advanced in the note to § 24), that the muscular substance and the sarcolemma are homologous with the matrix of cartilage; that, in short, as the elastic and collagenous elements of connective tissue are the results of the chemical and morphological differentiation of the matrix of the primitive embryonic tissue,—so, the sarcous elements and the sarcolemma are the products of a corresponding differentiation of the same primitive element.

What that primitive matrix is, is a question, the consideration of which we must defer as we have done before; that it is not "cell-contents," however, is sufficiently obvious.

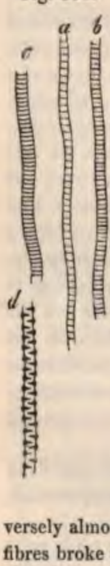
The fibres of the fœtus figured above, broke up into discs very readily while quite fresh, and thus exhibited the peculiar dotting produced by the sarcous elements (fig. 3). Many of the fibres appeared to have the edges of the discs double, as in fig. 1. After a day or two (the weather being cold), the disposition to cleave trans-

Fig. 107 *A*. 1, 2, muscular fibres from a seven-months' fœtus; 3, discs, viewed in section; 4, so-called muscle-cells, from the triceps of the same fœtus; 5, junction of the triceps with its tendon: *a*, "nuclei;" *b*, bundles of connective tissue.

§ 87.

Physiological Remarks.—The most remarkable peculiarity of the muscles is their *contractility*. In each contraction, the primitive fasciculi shorten themselves in a rectilinear direction, and at the same time become thicker; they do not, however, undergo any considerable condensation. It is probable, that the contractions generally take place simultaneously in every part of a fasciculus, although at the same time it is not, of course, intended to be said, that the contraction does not commence at the points where the terminations of the nerves occur, and that this contraction does not precede, though by a space of time immeasurably short, or at all events inappreciable by the eye, that of the other portions of the fasciculus. Under certain conditions, however, *successive, progressive,* and *partial* contractions are observed. If, during the contraction of a muscle, its longitudinal and transverse striæ are noticed, it is not difficult to show that where the former exist, they disappear during the contraction, and give place to transverse markings; and that the latter, where they were already present, become more distinct, and more closely approximated. Moreover, in the easily isolated fibrils of the thoracic muscles of insects, it is easy to perceive that they exhibit very variable conditions in different animals, and vary frequently in one and the same individual. Sometimes they are almost without transverse markings, and very pale; sometimes darker, and with distinct transverse lines; sometimes, again, very distinctly ringed; and, together with these varying conditions, does the thickness of the fibrils and the distance between the transverse

Fig. 108.



versely almost ceased, while the transverse marking became less distinct, and the fibres broke up very readily into fibrils (fig. 2). In this condition they often resembled the smooth muscles of mollusks.

Fig. 108. Primitive fibres from the alar muscles of the "Dung-Fly," × 350 diam.: *a*, slender fibril, with very distant delicate transverse striæ; *b*, thicker fibre, with closer, alternately stronger and fainter striæ; *c*, still thicker fibril, with the striæ more closely approximated; *d*, fibril with lateral, alternate elevations (they have come out too dark).

striæ, vary also; so that the fibrils which exhibit the most distinct striation, are almost as thick again as the others, and their transverse striæ are placed almost twice as closely together. It may thence, perhaps, be allowable to conclude, that in the act of contraction the principal phenomenon consists in the shortening and thickening of the fibrils, and also, that the changes in the fasciculus above noticed depend upon these changes in the fibrils. The further question now arises: how is this shortening of the fibrils effected? and whence does the transverse striation arise? Is the latter connected with the vital conditions of the muscle, or is it produced independently of these? It is unnecessary to answer the latter query in the affirmative, for *dead* muscles exhibit transverse striæ, and indeed, under the same conditions as the living. This is best shown in muscles successively subjected to various degrees of tension; and consequently, all notion of a merely partial contraction of the fibril, which arises on the first observation of these conditions, must be relinquished. The transverse striation is manifestly merely a physical, not a vital phenomenon. It arises, either because the fibrils are *not homogeneous* throughout their whole length, but divided into *numerous small segments*, some of which are possessed of greater elasticity than the others; or, in the opposite case, it may depend upon the circumstance, that the fibrils are soft filaments, which, in shortening, become curved in a zigzag or wavy manner, or varicose. Which of these two views is the correct one, cannot at present be determined; and this much only can be said, that in favour of the former supposition, the fact can be adduced, that fibrils, after maceration, readily break up into minute particles (*sarcous elements*, Bowman), and possibly consist of a series of such elements connected by a heterogeneous interstitial substance; whilst in favour of the second, are the conditions presented in the fibrils of connective tissue, which are undoubtedly homogeneous throughout, and yet when made to contract by the application of acetic acid, exhibit extremely delicate transverse markings, in consequence of which, the fasciculi composed of them frequently offer a deceptive resemblance to those of striped muscle. It is difficult to say whether the sarcolemma participates actively in the shortening of the fibrils, although, especially from the consideration of its chemical and physical

properties, which approach those of elastic tissue, I am rather inclined to the opinion, that its function, in the contraction of the fibre, is merely passive. The same may with greater certainty be affirmed of the albuminous fluid uniting the individual fibrils. Consequently, it is not the muscular fasciculus, *in toto*, but only the fibrils, which are to be regarded as the contractile elements; a position which is not shaken by the circumstance, that other conditions occur in the smooth muscles, and in many muscles in the Invertebrata (those that exhibit no fibrils).

This is not the place to dilate upon the causes to which the contractions of the muscles are due, and by which they are necessarily produced, and I will merely offer the following remarks. There can be no doubt that the contractility of the muscular substance is a proper and inherent attribute, and only called into manifest action to a certain extent through the nerves; whilst it is equally certain, that there are no facts which conclusively demonstrate, that the striped muscles contract independently of a previous nervous influence. What the processes are which take place in the fibrils during the contraction is wholly doubtful; but it is to be hoped that the further investigation of the laws of the electric currents in the muscles, prosecuted in the way so successfully pursued by Du Bois Reymond ('Untersuchungen über thier. Electricität,' Berlin, 1848-49), will throw some light upon this, as yet, obscure subject. It would be more than bold to hazard an assertion with respect to the nature and mode of action of the nerves upon the muscles, since we are quite as much in the dark as to the processes which take place in the nerves, as we are with regard to those occurring in the muscles themselves. From the anatomical facts, which prove, that in many animals the motor nerve-fibres come in contact with each primitive muscular fasciculus only at a few points, and never penetrate into its interior, it is, however, rendered evident, that in the contraction of a muscle, the nervous influence must act from a certain distance.

The muscles also possess sensibility, though of a rather peculiar kind, because punctures, burns, and incisions into their substance, excite scarcely any sensations worth naming, whilst every muscle, after long-continued activity, as well as

when affected with cramps or spasms, becomes painful and very sensitive to pressure. They are also endowed with an extremely delicate sense of feeling for their own state of contraction, so that they are capable of estimating very minute variations in the force with which they act. The apparent contradiction between these facts is easily accounted for, by the consideration that the muscular nerves contain but very few sensitive fibres, as is readily shown in the nerves of the orbital muscles, &c. These fibres, to which probably belong the few filaments above described, which are distributed over the whole muscle, though too scanty to render a muscle sensible to local impressions, nevertheless suffice, when implicated in the contraction of the entire muscular substance, to convey to the sensorium the degree of pressure to which they are subjected, and, when the organs are over-exerted, to induce pain, in consequence of the frequently-repeated irritation which they have undergone, or of the compression they endure from the rigidity of the muscle.

[The mechanical relations of the muscles have been excellently treated of in the article by E. Weber (l. c.), from which the following conclusions may be drawn. The extent of the shortening of the muscles amounts, in experiments upon animals, on the average to $\frac{3}{4}$ths, or in powerful muscles even to $\frac{5}{6}$ths. The contractile force of a muscle does not depend, *cæteris paribus*, upon its length, but solely on its transverse sectional area; that is to say, on that of all its primitive fasciculi, so that a longer and a shorter muscle exert the same force, when the sum of the transverse sections of all the fasciculi is the same in both. According to the observations of Schwann and Weber, the elasticity of the muscles diminishes at each contraction, and consequently the molecular motions, called into play in them under the nervous influence, must be connected with a change in their substance of an altogether peculiar kind, which, however, can certainly only be regarded as a secondary effect. The degree of contraction differs according to the amount of antagonism with which it meets; if the latter be sufficiently powerful, no true movement of the limb takes place, that is to say, the points of origin and insertion of a flexor muscle (for instance) do not approximate; never-

theless, the fibres themselves contract to a certain extent, in consequence of which the whole muscle becomes tense. This tension must be carefully distinguished from that dependent upon the muscular elasticity, which is generally much less considerable. What has been termed the "tone"—*tonus*—of muscles, does not in most cases depend upon contraction, but is an elastic tension; I therefore hold, that the posture of the body and the occlusion of the transversely striated sphincters during sleep, has nothing to do with a contraction of the muscles, although such contraction is indubitably requisite to bring the body into this posture. In my opinion, during sleep, all the muscles (of course, with the exception of the respiratory) are at rest, being held in a state of tension, and of antagonism to their opponents merely by their elastic force, and are consequently in the condition of a muscle when supported, in a person in the waking state. As for instance, a *biceps*, when the arm is bent, may immediately lose its tension if the arm be supported, so in the same way may all other voluntary muscles; only it must not be forgotten, that such a condition of muscular rest may ensue upon all conceivable degrees of contraction. Even the *orbicularis oris*, when contracted, may be at rest and lose its vital tension. The mouth, nevertheless, will remain closed, for this reason, that although the elastic force, as always after a contraction, will not fail to exert a certain degree of extension upon it, it is unable to open the mouth, owing to its limited amount and inability to overcome the weight of the lips. I do not believe in any muscular "tone," if under that term be understood a long-continued involuntary contraction (though at first excited by the will); but am of opinion, that what has been most generally described under this name, is merely an elastic tension, which has been confounded with the contraction upon which it has ensued. From all we know, the nerves are incapable of exciting a long persistent contraction in the striped muscles, but very capable of producing great effects, when the states of contraction and of rest are duly alternated, as for instance in walking, running, &c., and in the heart and respiratory muscles.

The importance of this view of the nature of the muscular "tone," as regards the physiology of the nerves, is sufficiently

obvious; but in pathology also, it may be employed, in explanation of the retraction of divided muscles, and the shortening which takes place in muscles whose antagonists are paralysed. The former, as correctly pointed out by E. Weber, depends upon the elastic force, and takes place, as far as I know, only in extended, tense muscles, but not in those which are in a state of contraction, which, on the contrary, when cut across, immediately become lengthened, as may be readily observed in the Frog. It is quite true, that contractions also take place in divided muscles, in consequence of nervous influence; but these are never more than local, and cease without the production of any important effect on the form of the wound in the muscle.

The shortening which occurs in the antagonists of paralysed muscles, is not referable either to the elastic force of the non-paralysed muscles, which is much too slight to influence the position of a limb, or to their persistent "tone," but depends simply upon the voluntary innervation of the muscles, which are still in an active condition, and which, no longer meeting with any opposition from their antagonists, draw the limb in their own direction. The persistence of the oblique position which now ensues, may be readily explained without our necessarily assuming the existence of a permanent contraction, when it is considered that muscles, the antagonists of which are paralysed, never again become elastically tense. In lead-palsy, for instance, when the first contraction of the flexors, consequent upon the paralysis of the extensors, ceases, the former, even under the most favorable circumstances, become extended only so far as to assume their natural form, a condition from which necessarily results the semiflexed position of the part affected. In accordance with this view, I regard the permanent condition of the unaffected side of the face, in one-sided paralysis of the facial nerve, and that of the upper eyelids in blepharoptosis, as produced, not by a persistent contraction, but as indicative of a state of perfect rest in the muscles, except when voluntary movements take place. The falling of the upper eyelid is explained by the paralysis of the *levator*, and the inability of the *orbicularis*, by its extension after a previous closure, to raise the eyelid beyond a certain point. In the same way the distortion of

the face is produced, at first by the voluntary contraction consequent on the paralysis, upon the cessation of which it is impossible that the previous symmetry of the features should be restored, because the antagonist muscles on the opposite side are paralysed, and their slight elastic force during life is insufficient, simply upon the cessation of the contraction, to restore the pristine position of the lips, angle of the mouth, &c. An actual distortion, therefore, dependent upon persistent muscular contraction, can only take place in consequence of morbid conditions of the central organs.

In the *investigation* of the muscles it is necessary that they should be studied in the fresh state, and with the aid of various reagents. The primitive fasciculi are most easily isolated in muscles which have been boiled or immersed in spirit, in which also, the transverse striæ are for the most part very well displayed, as is also the case after treatment with corrosive sublimate or chromic acid. In the study of the transverse striæ, it is above all indispensable that the muscles should be viewed in various degrees of extension and contraction (fig. 109). The former conditions, which are well worth observation, are readily viewed, if long slender muscles, such as the *hyoglossi* of the Frog, &c., are examined on a wooden stage having a central opening filled in with glass. It will then be seen, when no extension whatever is employed, that the transverse striæ are narrow (about 0·0004‴) and very closely approximated, and that the fasciculus itself is broad; whilst, when it is extended to the utmost, the stripes are 0·0008‴ wide, and placed at the same distance apart, and that the fasciculus is narrower. The *contractions* must be observed either in fresh muscles still quivering, and kept moist with serum, albumen, or vitreous humour; or in the way proposed by E. Weber,—and which consists in the galvanizing, by

Fig. 109.

Fig. 109. A primitive fasciculus of a Frog's muscle in different degrees of extension, × 350 diam.: *A*, the fasciculus, stretched and slender, with broad distant transverse striæ; *B*, the same not extended, broader, and with narrower, closely approximated striæ.

means of the rotation apparatus, of the muscle to be examined, such, for instance, as the abdominal muscles and slender muscles of the extremities in the Frog, the diaphragm and cutaneous muscles of the smaller Mammalia, &c. For this purpose the muscle must be placed upon a piece of looking-glass, from a small space in the middle of which the metallic coating has been removed. One of the conducting wires is brought through an opening in the stage, or else affixed to it so as to be immoveably in contact with one of the portions of tinfoil. If the muscle now be viewed under a magnifying power of 100 linear, whilst the second conducting wire is brought in contact with the other portion of tinfoil, the moment the circuit is completed, its fibres will be seen to contract in a rectilinear direction, and at the same time to become thicker, whilst the transverse striæ are more closely approximated (*vide* fig. 109, which represents both a contracted and an extended muscle). The muscular fibres remain in this condition so long as the galvanic influence is kept up, whilst when the circuit is broken they elongate themselves as rapidly as they contracted, and present zigzag flexures, when the muscle is lying free, but not when it is stretched by small weights attached to it by threads. From this it is evident, that if zigzag flexures take place during life, which is not yet known to occur, they can only arise when muscles in the quiescent condition are not in a state of tension; as, for instance, in the case of a flexor muscle, which has come into a state of rest after it has produced its full effect upon the limb. The *sarcolemma* is readily seen in the muscles of Amphibia and Fishes, especially in specimens preserved in spirit, in which it frequently, but for the most part in places, appears at a distance from the fibrils. In the higher animals and in man, it is occasionally seen when the fasciculi are teased out; and also in macerated and boiled muscles, and on the addition of acetic acid or alkalies. For this purpose I would especially recommend caustic soda, which in many cases renders the contents of the muscular tubules so fluid, that they escape in a continuous stream together with the nuclei, when the sheaths come very clearly into view. In no case, however, is the *sarcolemma*, in man, more beautifully exhibited than it is, in softened, atrophied muscles which have undergone fatty or other degeneration;

and, in fact, the greater the degree of degeneration, the more distinctly is this structure exhibited. The muscular fibrils, in fresh muscles, are constantly visible only in a transverse section, and in the thoracic muscles of insects, elsewhere it is true they are occasionally seen, but more by chance than otherwise. They are easily isolated artificially in preparations preserved in spirit, particularly in the perennibranchiate Reptiles (*Siredon, Proteus,* &c.), by treatment with chromic acid (Hannover), by maceration for from 8 to 21 days, at a temperature of 1—8° R. in water, to which, for the prevention of putrefaction, some corrosive sublimate has been added (Schwann); maceration also in the fluids of the mouth (Henle) allows of their being readily exhibited; whilst, according to Frerichs (Wagner, 'Handwörterb.,' III, 1, p. 814), in the stomach, the fasciculi break up into Bowman's discs. The nuclei of the fasciculi are best studied under the application of acetic acid; by soda (*vide supra*) they may be isolated, and by potass be made to swell considerably (Donders). On the subject of the effect of various reagents on the elementary tissues of muscle, the treatises of Donders (Holländ. 'Beiträge') and Paulsen ('Observ. microchem.,' Dorpat, 1849) may be consulted. The *vessels* of muscle are studied in fresh, thin muscles, and in injected preparations; the *nerves* in the smallest human muscles, in the muscles of the smaller Mammalia, in the cutaneous muscle on the thorax of the Frog, with or without the addition of soda. The *perimysium,* and the form and position of the muscular fibres, are very well shown in transverse sections of half-dried muscles; and the same observation holds good with respect to the elementary tissues of the *tendons.* The insertions of the latter into the bones, and their cartilage-cells in those situations are readily seen; in the *tendo Achillis,* for instance, in vertical sections of dried preparations; with respect to their relation to the muscular fasciculi, *vide supra,* § 81. In order to examine the cartilage-cells in tendons, thin horizontal sections are taken from the surface, which are treated with acetic acid, or a very dilute solution of soda. For the study of the development of muscle, the naked Amphibia must be placed in the first rank, and the Mammalia only in the second.]

Literature.—Besides the memoirs, cited in § 27, there are

to be mentioned: G. Valentin, article 'Muscles,' in the 'Encyclopædic Dictionary of the Medical Sciences,' vol. xxiv, pp. 203—220, Berlin, 1840; H. R. Ficinus, 'De fibræ muscularis formâ et structurâ Diss. inaug.,' Lips. 1836. 4, cum tab.; F. Will, some remarks upon the origin of the transverse stripes of muscles, in Müller's 'Archiv,' 1843, p. 358; R. Remak, on the 'Development of the Primitive muscular Fasciculi,' in Froriep's N. Notiz.,' 1845, Nr. 768; Ed. Weber, art. 'Muscular Motion,' in R. Wagner's 'Manual of Physiology,' vol. iii, 2d division, 1846; Kölliker, in 'Ann. d. Sc. Nat.,' 1846; Dobie, 'Observations on the Minute Structure and Mode of Contraction of Voluntary muscular Fibre,' in 'Ann. Nat. Hist.,' N. Ser. III, 1849; Lebert 'Recherches sur la Formation des Muscles dans les Animaux vertebrés, in Ann. d. Sc. N.,' 1850, p. 205.

OF THE OSSEOUS SYSTEM.

§ 88.

The *osseous System* consists of a great number of hard organs, the *Bones*, of a peculiar, uniform structure, which are united either immediately or by means of other tissues, such as cartilage, ligaments, or articular capsules, into a connected whole—the *skeleton*.

The osseous tissue, in man, presents two principal forms—the *compact* and *spongy*. The perfect solidity of the former, however, is only apparent, as, even to the naked eye, it is seen to be penetrated by narrow channels which run in various directions, and by a still greater number of similar but smaller canals, which are brought into view by the microscope. These *vascular* or *Haversian canals* (medullary canals of authors), may be said to be almost entirely absent in the spongy substance, in which they are represented by wider, rounded, or elongated spaces, visible to the unassisted eye, which are filled with marrow, in some bones occupied by veins or nerves (*cochlea*), and termed the medullary spaces or cells (*cancelli, cellulæ medullares*). These spaces all anastomose together, and are formed by the reticular arrangement of the small

quantity of osseous tissue, which is disposed in the form of fibres, laminæ, and small rods. When the spaces are of a larger size, the substance is termed *subst. cellularis,* and when smaller, *subst. reticularis.* The latter, in some situations where the cavities are smaller, and the osseous partitions stronger, approaches in character the compact substance, although it does not actually become such; and in others it passes without any defined limit, into compact tissue. This does not, however, prove that the two substances are identical, but, as we learn from observation of their development, depends simply upon the circumstance that the spongy substance very frequently arises in a partial expansion of the compact. The share taken by the two substances in the formation of the different bones, and parts of bones, varies very considerably. It is only in a few situations that the compact substance is met with by itself without vascular canals—as in the *lamina papyracea* of the ethmoid bone, some portions of the lachrymal and palate bones, &c. It occurs more frequently, however, with vascular canals, and without spongy substance, as in many individuals in the thinnest portion of the *scapula, ilium, acetabulum,* cranial bones (*ala magna, parva* of the sphenoid, the orbital process of the frontal bone, &c.). Spongy substance with a thin compact cortex, without vascular canals, exists in the auditory bones, on the surfaces covered with cartilage of all bones, probably also in the smaller spongy bones. In all other cases, and consequently in most situations, the two substances are conjoined, but in such a way, that sometimes the spongy substance predominates (spongy bones and parts of bones), as in the *vertebræ,* carpal and tarsal bones; sometimes the compact, as in the *diaphyses* of the long bones; or the two are in equal proportions, as in the flat bones.

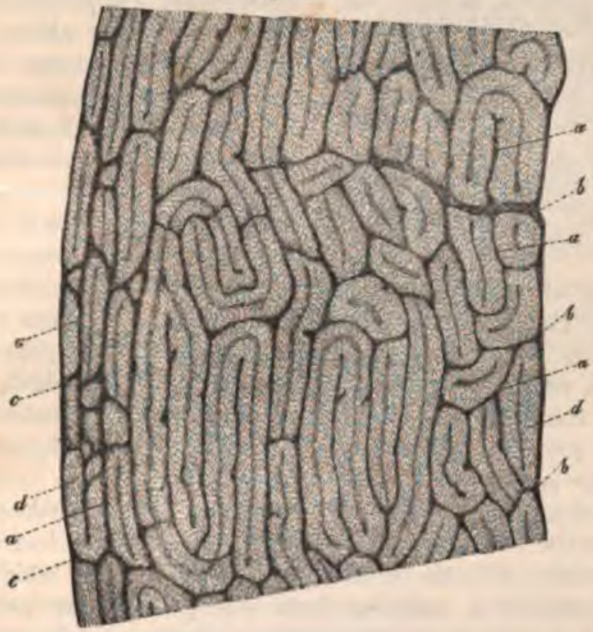
§ 89.

Intimate structure of the osseous Tissue.—The osseous tissue consists of a dense, for the most part indistinctly lamellar fundamental substance or matrix, penetrated by vascular canals and numerous minute microscopic spaces—the *bone-cells, or lacunæ* (bone-corpuscles of authors), having very minute hollow processes, the *bone-canaliculi.*

The vascular canals of the bones, or the Haversian canals

(*canaliculi medullares*), are minute tubules, having an average diameter of 0·01 — 0·05‴, and in the extremes one varying from 0·004‴ to 0·18‴, and which, except in the thinner parts of the facial bones, as above mentioned, exist universally in the compact substance, forming in it a wide network similar to that of the capillaries. In the long bones, and also in the ribs, clavicle, *pubis*, *ischium*, and lower jaw,

Fig. 110.

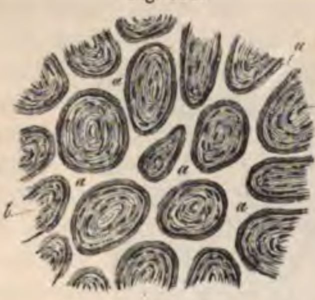


they run chiefly in a direction parallel to the long axis of the bone, and, as shown in longitudinal sections, either parallel to the surface or perpendicular to it, at distances varying from 0·06‴ to 0·14‴ apart. They are connected by transverse or oblique branches, which run in the direction both of the radius and of the tangents of a transverse section of the bone. Consequently, under a low magnifying power, in longitudinal sec-

Fig. 110. Segment of a transverse section from the shaft of the *femur* of an individual 18 years old, × 350 diam.: *a*, Haversian canals; *b*, their openings internally; *c*, externally; *d*, osseous substance with lacunæ. In this figure transverse sections of vascular canals and fundamental lamellæ are not shown.

tions of one of those bones, either parallel to the surface or perpendicular to it, closely approximated canals running parallel to each other, chiefly in a longitudinal direction, are seen, here and there with connecting branches, and thus forming a network, consisting of elongated, and most generally, rectangular meshes (fig. 111). And in a transverse section—transverse sections of the canals, placed at tolerably definite but small distances apart, are principally apparent (fig. 112); which, more especially in younger bones, are occasionally connected by a tangential branch, and some anastomoses in the direction of the radius. In transverse sections of fœtal and undeveloped bone (in man even at the age of eighteen), scarcely any transverse canals occur, but chiefly those running horizontally in the direction of the tangents and radius (fig. 110), so that the bones appear to consist entirely of short thick lamellæ, each of which, upon closer examination, is seen to belong to two canals, and exhibits a pale central line, indicating the division between the two constituent portions of which it is formed.

Fig. 111.



In the *flat bones*, the greater number of the canals do not run in the direction of the thickness of the bone, but almost all, parallel with its surface, and indeed in lines which may be conceived as radiating from one point (*tuber parietale, frontale,* upper and anterior angle of the *scapula,* articular portion of the *ilium*) in a penicillar or stellate manner towards one or several sides; or less frequently, as in the *sternum,* are all parallel to each other. In the short bones, lastly, there is most usually one predominant direction in which the canals run, as the vertical in the vertebræ,—that of the long axis of the extremity in the carpal and tarsal bones, &c.; it must be remarked, however, that the larger processes of these bones, as, for instance, the spinous processes of the vertebræ, differ in

Fig. 111. Haversian canals from the superficial lamellæ of the *femur* of an individual 18 years old, treated with hydrochloric acid, × 60 diam.: *a*, canals; *b*, osseous substance with lacunæ.

this respect from the rest of the bone, and, like those of other bones, such as the coracoid and styloid processes, exhibit the same disposition of the canals as that which exists in one of the shorter cylindrical bones. The lamellæ, fibres, and bars of the spongy substance, occasionally present a few vascular canals, but only when they are of some thickness.

As the Haversian canals are vascular channels, they open in certain situations: 1. externally, on the outer surface of the bone; and, 2. internally, on the walls of the medullary cavities and spaces. In both situations, excessively fine and coarser pores may be every where perceived, partly visible to the naked eye, and which are more numerous in proportion to the thickness of the cortex of the bone. But the relation of the vascular canals in the compact substance to these canals thus proceeding from within and without, only partially resembles that between the branches and trunks of vessels, and only in the outermost and innermost lamellæ of the cortical substance. In the interior of the cortical portion of a bone the canals are independent, and morphologically may be most aptly compared to a capillary network, which at its borders is in connection at many points with larger canals. Where the cortical substance rests upon the spongy substance, as in the interior of the ends of the *diaphyses*, and in the lateral periphery of the *apophyses*, the vascular canals are continuous, sometimes abruptly, sometimes quite gradually, expanding in an infundibuliform manner, and frequently anastomosing, with smaller or larger medullary spaces, so that, very often, no definite limit is perceptible between them. I have never yet noticed cæcal terminations of the vascular canals; it is, however, certain, that in many situations on the surface they must constitute, over extensive spaces, closed networks, especially where very few or no vessels enter the compact substance, *as at the points of insertion of many tendons and ligaments, and beneath several muscles* (temporal).[1]

[1] [A most valuable contribution to our knowledge of the structure and development of Bone has lately been made by Messrs. Tomes and De Morgan, in their 'Observations on the Structure of Bone,' read before the Royal Society in June, 1852, but not yet published. We are enabled, however, by the kindness of those gentlemen in allowing us to inspect many of their preparations, and in furnishing us with the proofs of their paper, to make some very important additions and corrections

§ 90.

The *matrix* of bone is lamellar, and the lamellæ (fig. 112) are apparent in thin sections, but are still better shown in bones from which the earthy matter has been removed, or which have been exposed to the weather or calcined, in which cases the lamellæ exfoliate, and, in the cartilage of decalcified bones, may even be raised with the forceps. In the middle portions of the cylindrical bones they constitute two systems—one *general,* in which the lamellæ are parallel with the external and internal surfaces of the bone, and *numerous special ones,* around the separate Haversian canals. These two systems are in some places in immediate connection, but in most, merely in apposition, and on that account they may conveniently be regarded as of two kinds; a view with respect to them, which is in some degree supported by the phenomena presented in their development.

to the text. We may add, that although we do not always agree with Messrs. Tomes and De Morgan in the interpretation of the facts, differences which we shall duly note, our own investigations have led us to believe that their paper is by far the most accurate account of the process of ossification which has yet appeared.

These writers have pointed out the important fact, that besides the well-known Haversian canals, other cavities exist in bone, which they denominate *Haversian spaces.* These have irregular outlines similar to that of the surface of exfoliations, while the boundaries of the Haversian canals are always more smooth and rounded. Again, in the latter, the laminæ are more or less conformable with the canal; while the walls of the *spaces* are formed by the unconformable edges and surfaces of the laminæ of the adjacent Haversian canals, which have, as it were, been eaten away to form the *space.* In fact, bone, so far from being a permanent or stationary structure, is continually being deposited, and as constantly re-absorbed. The Haversian spaces are the result of the absorption of previously existing osseous tissue; but when this process has gone on to a certain extent, deposition commences in the spaces, and they are converted into Haversian canals. The calibre of these canals now becomes narrowed up to a certain point by the continual laminar deposition of ossific matter; which, after a while, is traversed by new absorptive tunnels, or Haversian spaces, and is removed in its turn.

The spaces are very numerous and large in newly-formed bone situated near ossifying cartilage; while, in older bone, they are far less frequent and generally smaller. They are, however, never absent; being found even in old subjects. They may be observed in various conditions in a series of sections. In one place the space will have attained a large size, while in another part of the same section, its commencement will be seen extending from one side of an Haversian canal. One side of a space may be becoming the seat of a new system, while the opposite is undergoing further enlargement.—Eds.]

The lamellæ of the Haversian canals (fig. 112 *c*, 113 *b*) surround those canals concentrically, in greater or less number. They constitute, as it were, the walls of the canal, and are intimately united to each other, much in the same way that the laminæ of the walls of the larger vessels are continuous with each other. The number of lamellæ belonging to a canal, and the collective thickness of the system formed by them, varies not inconsiderably, and bears no constant relation to the size of the canal, as is the case to some extent in the vessels; small canals, therefore, are not unfrequently surrounded by numerous lamellæ, and larger ones by but few.[1] In general, it may be said, that the largest canals have thin walls, those of a middle size thick ones, and the most minute, again walls of little thickness. The thinnest walls I have commonly noticed, measure 0·008—0·02‴, and the thickest 0·08—0·1‴. The thickness of the lamellæ varies between 0·002 and 0·005‴, being on the average 0·003 to 0·004‴; in number, there are usually from eight to fifteen; sometimes,

Fig. 112.

Fig. 112. Segment of a transverse section of a human metacarpal bone, treated with oil of turpentine, × 90 diam.: *a*, external surface of the bone, with the exterior fundamental lamellæ; *b*, internal surface towards the medullary cavity, with the inner lamellæ; *c*, Haversian canals in transverse section with their lamellar systems; *d*, interstitial lamellæ; *e*, lacunæ and processes.

[1] [The "interstitial laminæ" are the remains of Haversian systems, the larger parts of which have been removed by absorption to form new spaces. The irregular outline of the outermost of the *laminæ* of a Haversian canal (see fig. 113) results from its being the first deposition within the pre-formed irregular Haversian space. (Tomes and De Morgan, l. c., p. 5.)—Eds.]

however, no more than four or five, and occasionally as many as from eighteen to twenty-two.

The lamellæ of the Haversian canals, together with their canals, extend to the internal and external surfaces of the *diaphyses*, where they are connected with the general lamellæ above mentioned—the *fundamental lamellæ* (fig. 111). The latter constitute an *external* and an *internal* layer, and penetrate also into the substance of the *diaphysis*, where they are interposed between the separate lamellar systems and the medullary canals. The two former layers, or the *external and internal fundamental lamellæ*, are parallel to the external and internal surfaces of the bone, and vary in thickness apparently without any definite rule, from 0·02‴ to 0·3‴, or even 0·4‴. The latter, or *interstitial fundamental lamellæ*, are seen most clearly where the superficial fundamental laminæ are developed, in partial connection and parallel with which they extend from without inwards, and from within outwards, some distance into the substance of the *diaphyses*, where they are interposed in masses, varying in thickness from 0·02 to 0·12‴,

Fig. 113.

Fig. 113. Portion of a transverse section of the shaft of the humerus, × 350 diam., treated with oil of turpentine: *a*, Haversian canals; *b*, their lamellar systems, each lamella presenting a more transparent and more opaque portion, with radiating striæ in the latter; *c*, darker lines, which probably indicate greater intermissions in the deposition of the osseous substance; *d*, lacunæ without visible rays. From a preparation by Dr. H. Müller.

between the other lamellæ (fig. 112, *d*). In the interior of the compact substance, on the other hand, in man, the Haversian systems are so closely crowded, that there can be no qnestion as to the non-existence of lamellar groups between them, and it is evident that those lamellæ, which in a transverse section appear in man to be parallel with the surface, almost all belong to horizontal canals; and it is but rarely that distinct interstitial masses are seen, as is usually the case in other mammalia. The thickness of the separate lamellæ just described is much the same as that of the lamellæ of the Haversian canals, and their number varies from 10 to 100.

We have hitherto considered only the *diaphyses* of the long bones. In their *apophyses*, the thin cortical layer of compact substance naturally presents only a few systems of Haversian canals, which, however, are constituted as elsewhere. The exterior fundamental lamellæ are few in number, and internally, owing to the existence there of the spongy substance, they are wholly wanting. In the latter substance, the very few Haversian canals present lamellar systems as usual, except that they are thin, and the remainder, according to the condition of the osseous network, consists of a lamellated and fibrous tissue, which in general follows the contour of the medullary spaces and cells. The *flat* and *short* bones present a similar arrangement *internally*, whilst the cortical substance of these bones differs from that of the cylindrical, only in the circumstance, that the fundamental lamellæ, in the flat bones, form layers parallel with both surfaces of the bone. The thickness of the fundamental lamellæ in the cranial bones (parietal), is sometimes the same in both aspects, and varies from 0·08‴ to 0·16‴, sometimes they are wanting in vascular situations, and in places, wholly so, on the external aspect of the bone, in which case the Haversian lamellæ reach almost to the surface.

With respect to the *intimate structure* of the osseous lamellæ, which is best studied in transverse sections, dried, polished, and sufficiently thin, there is usually evident, besides the bone-cells and canaliculi, in the generally not very distinct lamellæ, an extremely fine though very distinct punctated appearance, so that the whole osseous tissue appears granular, and to be composed as it were of separate, densely crowded, pale granules,

measuring 0·0002‴ (fig. 114). If water or weak syrup, or albumen, be applied to a slice of bone, it assumes a condition probably similar to that which it possesses during life. The lamellæ, for the most part (both in transverse and perpendicular sections), become clearly visible, and their granular aspect is quite distinct, although not so defined as before the bone was thus treated. For in the first place, together with the granules, there is exhibited a close, pale striation, referable to the canaliculi, which are filled with fluid, and which, extending in various directions through the tissue, renders its delineation more complex; there are also apparent in each lamella, as it were, two layers, one pale and more homogeneous, the other darker and granular, which latter chiefly is striated. When this condition is clearly displayed, an extremely delicate marking is produced, resembling that seen in transverse sections of certain urinary calculi (fig. 113). When once seen in moistened sections, indications of this arrangement will occasionally be observed in dried preparations. In bone treated with hydrochloric acid, the granules and striæ (dependent on the canaliculi), in sections both transverse and perpendicular to the surface, are less distinctly apparent, whilst the lamellar structure is very manifest, and most generally two layers may be noticed in each lamella, though by no means so clearly as shown in fig. 113.[1] In sections parallel to the surface, the bone, in

Fig. 114.

Fig. 114. Portion of a perpendicular section of a parietal bone, × 300 diam.: *a*, lacunæ, with pale, only partially-visible prolongations, filled with fluid as in the natural state; *b*, granular matrix. The striated places indicate the boundaries of the lamellæ.

[1] [According to Tomes and De Morgan, the laminæ, when well developed, are always constituted of two portions,—an outer, highly granular, often composed of a single line of large granules, and an inner, which is singularly clear and transparent, and to all appearance without granulation or any recognisable structure. This distinct separation into two layers, however, does not always exist; and in a complete Haversian canal, the innermost lamina of all is frequently clear, glassy, and structureless.

The circumferential laminæ are not so constantly present as is generally supposed,

many situations, appears almost homogeneous throughout, presenting no trace of a granular structure, whilst in others a structure of that kind is obscurely visible, together with minute points (Deutsch), and besides these a longitudinal striation; which last gives the whole a fibrous aspect. From this circumstance, many authors appear to have been led to describe the bone as composed of fibres, but quite incorrectly, for although the study of their development shows, that the ossifying parts are, to a certain extent, very distinctly fibrous, it is impossible to demonstrate anything of the sort in perfect bone. On the other hand, there is no doubt that a coarsely fibrous appearance exists, and especially in the bone-cartilage of the compact substance, as has already been remarked by others, and which is probably due to the fibrous fasciculi of the original blastema; care however should be taken not to look upon longitudinal sections of lamellæ as such fibres.[1] When

and they rarely entirely surround the shaft of a long bone, still more rarely the flat bones. In the fast-growing bones of young animals they are absent, while in adults they are usually well developed in some parts; so that their presence seems to indicate that the bone is nearly stationary in its growth. In young, rapidly growing bone, the circumferential laminæ are replaced by a series which may be called the *undulating laminæ*. The surface of the bone sends off processes, formed of reduplicated laminæ, which eventually arch over and inclose those vessels of the periosteum which lie nearest them. The spaces thus formed become the seat of Haversian systems. Young growing bone, therefore, may be distinguished from that of adult animals, by its being composed of Haversian systems with intervening undulating laminæ. (Tomes and De Morgan, l. c., pp. 4—6.)—Eds.]

[1] [Messrs. Tomes and De Morgan (l. c., pp. 13, 14) adduce very good reasons for believing that the fibrous appearance which may often be detected in the laminæ of bone arises from imperfect illumination and definition, and express their belief that bone substance "is composed of granules or granular cells, imbedded in a more or less clear, homogeneous or subgranular matrix." They go on to say, "Thus as regards the basement, homogeneous tissue, it will be found that where lamination is highly developed, the laminæ have a transparent and structureless, and a more opaque and granular part, to which the former appears to be the matrix. The peripheral lamina of the Haversian systems is generally clear and free from granularity, and the internal lamina sometimes presents a similar structureless appearance. The matter which fills up the Haversian systems in the full-grown antlers of the Cervidæ affords another and a very striking example of transparent structureless osseous tissue, which in this instance is the more distinct, from the absence of *canaliculi* in its substance. Then, again, we have another instance in the clear tissue which is sometimes found between the superficial Haversian systems of ordinary bone. It has already been described as a non-laminated element found on the surface of certain bones. In the instances already cited, and no doubt in many others which may be

bone is burnt and the fragments crushed, it affords, according to Tomes, minute angular granules, from $\frac{1}{5}$th to $\frac{1}{6}$th the diameter of the human blood corpuscle, and measuring, according to Todd and Bowman, $\frac{1}{8000}$th—$\frac{1}{14000}$th of an inch, and which are also rendered evident when bone is boiled in a Papins' digester. From these particulars, and from the granular aspect of fresh bone, which has also been noticed by Tomes and by Todd and Bowman, and moreover from the pretty nearly equal size of the granules visible in it, with those described by Tomes, and lastly, from the circumstance that bone treated with hydrochloric acid, as well as when calcined, both present a perfectly homogeneous substance without vacuities, it may be assumed that the osseous tissue consists of an intimate mixture of inorganic and organic compounds, in the form of closely connected minute granules.

§ 91.

Bone Cavities or Cells, and Canaliculi, (lacunæ et canaliculi ossium.)—In dried sections of bone, there are visible, scattered throughout the entire osseous substance, in all the lamellæ, microscopic melon-seed shaped corpuscles, with numerous, fine, ramified, and partially anastomosing rays, whose opaque and white colour (as viewed by direct light) is due, not to the deposition of calcareous salts, as was formerly supposed, and on

found in the skeletons of the lower vertebrata, we have bone tissue without obvious granularity, and without obvious structure; and although it forms but a small part of the general mass, yet from its constant presence at all ages and in all subjects, it must be regarded as an integral and normal part of mammalian bone. The granular condition of bone tissue is tolerably obvious in all preparations, though it is much more marked in some specimens than in others. The amount of the component granules varies in different parts of the same specimen, and in specimens taken from different parts of the skeleton. Thus, in one situation, we may see laminæ with a highly transparent part gradually merging into a transparent tissue, while in another the laminæ may be granular throughout. Again, in young bone developed in cartilage, the part between the cells becomes highly granular, fragments of which may be found in certain adult bones, as in the petrous portion of the temporal bone. Bone near the articular surface frequently presents a well-marked granularity."

We may remark, in addition to this very just account of the minute structure of bone, that, of the lower vertebrata above referred to, the Skate offers one of the best examples of structureless bone, in those polygonal plates which are developed (not on the surface, as is commonly said, but) in the interior of the cartilaginous skeleton. —Eds.]

which account they were termed "bone," or "calcareous corpuscles," but simply to their being filled with air. In fresh bone, not yet deprived of its watery constituents, nothing can be seen in these bone-cells or lacunæ but clear contents with a nucleus, which may best be described as the nutritive fluid of the bone, and consequently the designation above given to these cavities is the most suitable.

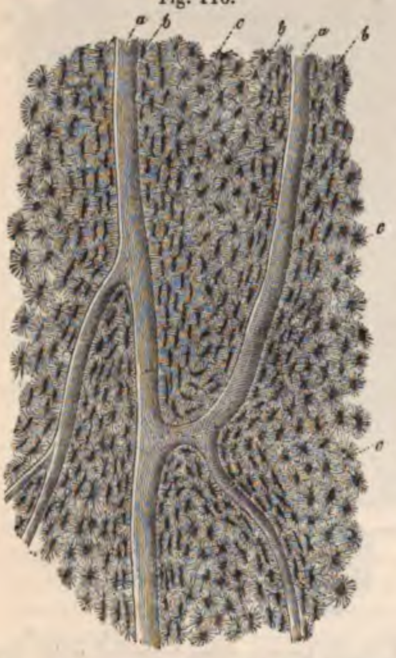
The *lacunæ* are elliptical, flattened cavities, having an average length of 0·01‴, 0·004‴ wide, and 0·003‴ thick, which give off both from the borders, and particularly from the surfaces, a great number of very fine canals, measuring 0·0005 — 0·0008‴ in diameter—the *bone-canaliculi* above-mentioned (figs. 115, 116, and 117). The lacunæ are equally numerous in both of the lamellar systems before described, and are placed so close together, that, according to Harting (l. c., p. 78), from 709 to 1120, or, on the average, 910 of them occur within the space of a square millimeter. They lie for the most part within the lamellæ, but also between them, and are invariably placed with their broad sides parallel with the surfaces of the lamellæ. The *canaliculi* proceeding from them are much branched, and penetrate the osseous substance in all

Fig. 115.

Fig. 115. From a transverse section of the shaft of the humerus, × 300 diam.: *a*, Haversian canals; *b*, lacunæ with their canals, in the Haversian lamellæ; *c*, lacunæ of the interstitial lamellæ; *d*, lacunæ with unilateral canaliculi proceeding to the surface of the Haversian system.

directions, their course being irregular, and often actually curved. They proceed principally, however, in the first place, from both surfaces of the lacunæ straight through the lamellæ; and secondly, parallel with the Haversian canals, from the two poles of the lacunæ. It is only in certain limited spots that these canaliculi present *cæcal terminations;* everywhere else some of them *anastomose* in the most various ways with the canaliculi of the neighbouring lacunæ, whilst others communicate with the vascular canals, the medullary cavities, and the medullary spaces or cancelli of the spongy substance, or open on the surface of the bone. *The entire osseous substance, therefore, is penetrated by a connected system of cavities and canaliculi,* by means of which the nutritive juice secreted by the vessels is conveyed into its densest tissue.

Fig. 116.



The lacunæ and canaliculi do not exhibit precisely the same conditions in every part of the bones. In the lamellar systems of the Haversian canals, as seen in a transverse section, the elongated lacunæ, by reason of their curvature, lie as it were concentric to the canal, and their excessively numerous pores or canaliculi necessarily produce a very close striation radiating from the vascular canal (fig. 115). The lacunæ are sometimes extremely numerous, sometimes more scanty; in the former case they are, for the most part, arranged in tolerably regular alternation, or one behind the other in the direction of

Fig. 116. Section parallel with the surface from the shaft of a human *femur*, × 100 diam.: *a*, vascular canals; *b*, lacunæ seen from the side, belonging to the lamellæ of these canals; *c*, lacunæ viewed on the flat side, in lamellæ which are cut horizontally.

the radius of the lamellar system ; but they are also frequently disposed very irregularly, either crowded together (*vide* the lower part of fig. 115), or separated by wider interspaces. In horizontal and longitudinal sections of Haversian canals (fig. 116), when the section has passed through the middle of a canal, the lacunæ appear narrow and elongated, and disposed in rows one behind the other, and in numerous layers parallel with the canal; and also furnished with numerous canaliculi, which proceed for the most part directly inwards and outwards (consequently transversely through the lamellæ), but partly in a direction parallel with the long axis of the canal. If the section strike the surface of a system, the superficial lacunæ come into view, presenting very elegant forms, rounded or oval (figs. 115 *d*, and 117), surrounded in an irregular manner by a

Fig. 117.

complete tuft of canaliculi, which look directly towards the observer, and consequently appear more or less shortened, and by a smaller number of other canaliculi distributed on the surface of the lamellæ. Occasionally, even in the thinnest parts of a section, there occurs a tuft of canaliculi, cut across transversely, and without the lacuna to which they belong, whence these portions of bone exhibit a sievelike aspect. All

Fig. 117. Lacunæ viewed on the flat side, with the canaliculi, from the parietal bone, × 450 diam. The spots on the lacunæ or between them belong to canaliculi, which are cut across, or are the openings of canaliculi into the lacunæ ; *aaa*, groups of transverse sections of canaliculi, each group belonging to a lacuna which has been destroyed in the making of the section.

the canaliculi arising from the inner aspect of the innermost lacunæ of an Haversian system, proceed towards the canal, with which they, by this means, communicate, as may be clearly seen in thin, perpendicular, and transverse sections of bones filled with air, and in the walls of medullary canals laid open longitudinally. From the borders and external aspect of the same lacunæ other canaliculi are given off, which perhaps occasionally terminate in blind extremities, but for the most part communicate with those of the neighbouring, and particularly of the outer lacunæ. The succeeding rows of lacunæ are all mutually connected in a similar way, and thus the network of canaliculi and lacunæ extends to the outermost lamellæ of the system, where the lacunæ either communicate with those of the contiguous systems or of the interstitial lamellæ, or terminate independently, in which latter case (fig. 115 *d*) all the canaliculi, or at least most, and the longest of them, proceed inwards, that is to say, towards the vascular canal, from which they derive their nutritive fluid.

In the interstitial osseous substance between the Haversian systems, when it exists in small quantity, the few lacunæ, frequently not more than from 1 to 3 in number, are disposed more irregularly, and also present a rounded form (fig. 115 *e*); when the interstitial substance is more abundant, and distinctly lamellar, the lacunæ are also disposed more regularly, with their sides parallel to those of the lamellæ. The canaliculi of these lacunæ, in like manner, communicate with each other, and with those of the neighbouring systems. In the outer and inner fundamental lamellæ, lastly, the lacunæ are all placed with their surfaces parallel with those of the lamellæ, and consequently looking, for the most part, inwards and outwards, or towards the centre and periphery of the bone. In transverse sections they precisely resemble those of the Haversian systems, only that they are but little or not at all curved, except in the smallest cylindrical bones. In longitudinal sections, whether perpendicular or parallel to the surface, they present the conditions above described, with this limitation, however, that a larger number of lacunæ, of course, are seen in the same space in the latter case than in the former, and also that the sieve-like aspect described above is more frequently observed, giving the bone considerable resemblance to certain sections of

teeth (fig. 117). The canaliculi of these lamellæ communicate, in part as usual with each other, in part open on the external and internal surfaces of the bone (fig. 118). At the points of insertion of tendons and ligaments into the bones, the canaliculi of the outermost lacunæ probably terminate in blind extremities; a condition which obtains in every case, in those parts of bones which are covered with cartilage (articular ends, ribs, surfaces of the bodies of the vertebræ, &c.) In the rods, fibres, and plates of the *spongy substance*, the lacunæ are disposed in every possible direction, but, for the most part, with their long axis parallel to that of the fibres, bars, &c., and with their flat surfaces directed towards the cancelli. They anastomose also, in these situations, by means of their canaliculi; and the most superficial lacunæ open freely into the cancelli.

Fig. 118.

[The size and shape of the lacunæ, in man, upon the whole, vary but little. By far the greater number are melon-seed shaped or lenticular, some, more fusiform or spherical. In sections of bone well filled with air, in which alone I have made my measurements, I find their average length to be 0·01—0·014‴, frequently under and above that size, or from 0·006 to 0·016‴, rarely 0·02 or even 0·024‴ (cranial bones, lower jaw). The breadth, measured in horizontal sections, is 0·003—0·006‴; in transverse, it is usually somewhat greater, or as much as 0·008‴, or even 0·01‴, because the limits between the canaliculi and lacunæ cannot always be accurately defined. Their thickness or depth, lastly, in the smallest lacunæ, is 0·003—0·004‴, and in the larger 0·002—0·004‴. The diameter of the spherical lacunæ is 0·006—0·008‴. The canaliculi are, on the average, 0·008—0·016‴ long, seldom less

Fig. 118. Portion of the surface of the *tibia* of the calf viewed on the external aspect, × 350 diam. The numerous points are the openings of the canaliculi; the dark, larger, indistinct spots indicate the lacunæ to which these canaliculi belong, appearing from a greater depth.

or more, up to 0·02‴ and 0·024‴; in diameter they measure 0·0004‴; at the finest extremities, 0·0005—0·0008‴; on the average, 0·0008—0·001‴, at their origin from the lacuna. Their true distance apart, in horizontal sections, in which they appear as holes, is 0·0008—0·002‴; in transverse sections, in which they produce the radiating striæ, in consequence of their being viewed in several planes, they appear to be somewhat closer together, or at distances varying from 0·0008‴—0·0012‴. The circumference of a lacuna, together with the radiating canaliculi belonging to it, forms an imperfect sphere, having a diameter of from 0·02‴ to 0·034‴; with reference to which, however, it must not be forgotten, that individual canaliculi transgress the usual length of the others, as I have, in fact, measured anastomoses between two lacunæ of the length of 0·04—0·045‴.

The *contents of the lacunæ,* according to the later investigations of Donders, Virchow, and myself, appear very closely to resemble those of the cells of cartilage during life; that is to say, they are a clear, probably viscid fluid, with a nucleus. If bone-cartilage be boiled in water or caustic soda for 1 or 2 minutes, these nuclei often show themselves very distinctly; or opaque corpuscles make their appearance, which must be regarded as the contracted cell-contents including the nucleus, and analogous to the corpuscles in cartilage. A peculiar phenomenon is seen to occur, when bone is macerated in hydrochloric acid, which was first noticed by Virchow in a diseased, and afterwards in healthy bone, and by myself in the *cementum* of the horse's tooth,—the lacunæ become *isolated,* having longer or shorter processes, and appear like independent structures, or a sort of stellate cells. This phenomenon seems to depend simply upon the circumstance, that the tissue immediately surrounding the lacunæ offers more resistance to the action of the acid than it does elsewhere. In the *cementum* of the horse's tooth, cells also enclosing the lacunæ, and even Haversian canals, may

Fig. 119.

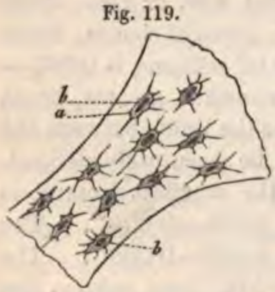


Fig. 119. A bone spicule from an apophysis, with distinct lacunæ and nuclei. Boiled in water, and magnified 350 diameters.

be isolated,—the best proof, that everything which thus presents itself in an isolated form, is not necessarily a morphological unity.[1]]

§ 92.

The Periosteum.—Among the soft tissues appertaining to bone, the *periosteum* is one of the most important. It is a more or less transparent, slightly glistening or whitish yellow, vascular, extensible membrane, investing a great part of the surface of bones, and contributing most importantly to their nutrition, by the numerous vessels which it sends into their substance.

[1] [It is of very great importance in histology to keep in mind the caution expressed in the last paragraph of the text (see below, note § 101), which applies as well to optical as to chemical distinctness.

Tomes and De Morgan assert that both the *lacunæ* and *canaliculi* have parietes, which are manifested by appearances similar to those observed in the dentinal tubes. They sometimes found the *lacunæ* and *canaliculi* filled up to a great extent with solid matter, so as to leave only a small space in the centre.

An important modification of the *lacunæ* is described and figured by these authors (l. c., p. 8) in the circumferential laminæ. Elongated tubes pass, in bundles or singly, more or less obliquely from the surface towards the interior of the bone. When long, they are sometimes bent once or twice at a sharp angle. They have parietes, and are connected laterally with the canaliculi. They occur irregularly in the circumferential laminæ, and in these only. [Similar tubes exist in the cementum of the Teeth.]

We can confirm Messrs. Tomes and De Morgan's statement that the nuclei may be found without difficulty in recent bone, and they may always be brought out with great distinctness by the action of dilute hydrochloric or strong acetic acid. This is especially the case in young bone. In old bone we have frequently been unable to discover them. Tomes and De Morgan, however, state that the nuclei are visible in sections of a fossil bone (supposed of a Pterodactyle) in their possession.

Another peculiar condition of the " lacunal cells," described by these authors, is their ossification. They found the light and spongy bones of old people to yield, if broken, a white powder, which was composed of large cells detached or united into masses. They are spherical, and contain a dark granular nucleus, which is surrounded by a thick transparent wall. Similar cells may be found adherent to the walls of the Haversian canals and *cancelli*; and in this case their nuclei have assumed the form of *lacunæ*, and the *canaliculi* of adjacent *lacunæ* advance into them. Similar cells may be found in most preparations of adult bone (l. c., p. 12).

We must confess that we doubt the assumption of a lacunal form by the "nucleus" in these cases. We have repeatedly examined these bodies, but if the nucleus was visible at all, we found it unchanged, and often adhering to one side of the *lacuna*. Again, it is questionable whether they may not rather be compared to the globules of dentine than to cells.—Eds.]

The *periosteum* is not, everywhere, constituted alike. Opaque, thick, and for the most part with the glistening aspect of tendinous structures where it is covered only by the skin, or is connected with fibrous parts, such as ligaments, tendons, *fasciæ*, and the *dura mater cerebri*, it is, on the other hand, thin and transparent in situations where muscular fibres arise directly from it without the intervention of tendon, and also on the *diaphyses*, where the muscles merely rest upon the bone, as on the external surface of the cranium (*pericranium*), in the vertebral canal, and in the orbit (*periorbita*). Where mucous membrane rests upon bone, the periosteum is, in most cases, very intimately united to it by the submucous connective tissue, so that the two cannot be separated, and constitute a single membrane, which, as in the palate, alveolar processes, nares, &c. is of greater, or, as in the maxillary sinus, tympanum, ethmoid cells, &c. of less thickness.

The connection of the *periosteum* with the bone itself is either more *lax*, consisting in simple apposition, and by more delicate vessels which penetrate the bone, or more *intimate*, taking place by means of larger vessels and nerves, and by numerous tendinous filaments. The former mode of connection is found especially where the periosteum is thin, and the osseous substance more compact, as in the *diaphyses*, on the inner and outer surfaces, and in the sinuses of the cranium; the latter, where the periosteum is thicker, and the compact substance thinner, as, for instance, in the *apophyses*, in the short bones, palate, and at the basis of the cranium.

With respect to the intimate structure of the periosteum, it will be found to present, almost universally, excepting where muscles arise directly from it, two layers, which, although closely connected, differ, more or less distinctly, in their structure. The outer layer is composed chiefly of connective tissue, with occasional fat-cells, and is the principal seat of the true periosteal vessels and nerves, whilst in the inner layer, elastic fibres, commonly of the finer sort, constitute continuous, and often, very thick networks—true elastic membranes—superimposed one upon another, the connective tissue forming the less important element. Nerves and vessels occur in this layer also, but they do little more than merely pass through it, being destined for the bone itself.

[The parts of the surface of bones unprovided with periosteum are: 1. The articular extremities covered with cartilage, and all other places where the bone is covered with cartilage or fibro-cartilage. 2. Where ligaments and tendons are attached to the borders and surfaces of bones at a certain angle, as, for instance, at the insertions of the *ligamenta flava, intervertebralia, iliosacra, interossea, teres ossis femoris, patellæ*, &c. of the tendons of the deltoid, *coracobrachialis, popliteus, iliopsoas, triceps suræ, quadriceps femoris, glutæi*, &c. In all these situations, the tendons, ligaments, and cartilages, are attached directly to the bone, as has been already in part described, and not a trace of periosteum can be detected.]

§ 93.

Marrow of the Bones.—Almost all the larger cavities in the bones are occupied by a soft, transparent, yellowish or reddish, highly vascular substance, the *Marrow* (*medulla ossium*). In the cylindrical bones, this substance is found in the medullary canal, and in the cancelli of the apophyses, whilst it is wanting in the compact substance, unless it be in the larger canals; the same is the case in the *flat* and *short* bones, the cancelli of which are filled with marrow; but the diploe of the flat cranial bones, besides the marrow, also contains large veins, of which more will be said afterwards. In accordance with what has been remarked, these venous spaces, the *canales nutritii*, Haversian canals, and the above-described nerve-canals and air-cavities of the bones, contain no marrow.

The marrow appears in two forms, one *yellow*, the other *red*. The former, as a semifluid substance, occurs principally in the long bones; and according to Berzelius, consists, in the humerus of the Ox, of 96·0 fat, 1·0 connective tissue and vessels, and 3·0 fluid with extractive matter, such as is found in muscle; whilst the latter occurs in the apophyses, flat and short bones, above all in the bodies of the *vertebræ*, the *basis cranii*, the *sternum*, &c., and is distinguished not only by its reddish or red colour and less consistence, but also by its chemical composition; for, according to Berzelius, this substance, in the *diploe*, contains 75·0 water, 25·0 solid matters, such as albumen, fibrin, extractive matter, and salts, similar to those of muscle, and merely traces of fat. With respect to its structure, it

presents, besides vessels and nerves, *connective tissue*, *fat-cells*, *free fat*, *a fluid*, together with, lastly, peculiar minute cells, *marrow-cells*. Connective tissue and fat are universally present, though in very various quantities. The former, on the surface of the larger medullary masses of the *diaphyses*, is of rather firmer consistence, but cannot properly be described as a medullary membrane (*endosteum*, *periosteum internum*), because it does not admit of being separated as a continuous structure. In the interior of the marrow in the spongy bones, scarcely any connective tissue can be detected except in the larger masses of it, whilst in the *diaphyses*, this tissue can be readily demonstrated as a very lax and delicate, areolated structure, containing the fat and supporting the vessels and nerves. Its elements correspond with those of the lax connective tissue (*vid.* § 24); although, as far as I have seen, it does not contain any elastic filaments. Fat-cells of 0·016—0·032‴, not unfrequently with a distinct nucleus, occur in large quantities in the yellow, more dense marrow, quite as abundantly as in the *panniculus adiposus*, but for the most part not aggregated into distinct lobules. In the reddish marrow, when expressed, they are more rare; and in the red pulp of the bodies of the vertebræ and of the flat cranial bones, they occur only in very minute, scanty accumulations, or altogether isolated, to which circumstance, according to Berzelius, is owing the small quantity of fat in the *diploe*. In dropsical marrow these cells are frequently only half filled with fat, or with but one or more globules, containing, besides, a large quantity of serum; and in hyperæmia of the bones, they appear occasionally to be diminished in size, and occasionally elongated and fusiform. *Free fat-globules*, and a clear or yellowish fluid, are often met with in the softer kinds of marrow, and frequently in considerable quantity. That the former have not been set free from cells, in the preparation of the specimen may be satisfactorily shown, but it must remain uncertain whether or not they are to be referred to cells that have ceased to exist. Lastly, there occur, together with some

Fig. 120.

Fig. 120. Two fat-cells from the marrow of the human *femur*: *a*, nucleus; *b*, cell-membrane; *c*, oil; × 350 diam.

fluid, in all the red, or even only reddish marrow (*never* in the yellow), minute roundish, nucleated cells, exactly like those of the young medulla (*vid. infra*, fig. 132). These medulla-cells correspond in every particular with those, which Hasse and I ('Zeitsch. f. ration. Medicin,' Bd. V) found in the hyperæmiated red marrow of the articular extremities of the cylindrical bones, but nevertheless normally exist in the *vertebræ*, the true cranial bones, in the *sternum*, and in the ribs, whilst they are wanting in the long and short bones of the extremities, and in the *scapula* and *os innominatum*, occurring apparently in variable number in the bones of the face.

§ 94.

Connections of the Bones.—*A. synarthrosis*, connection without articulation.

1. By *suture*. In this mode of connection, the bones are united by an extremely thin, membranous, whitish streak, to which authors have incorrectly given the name of sutural cartilage. It is composed merely of connective tissue, which, like that of the ligaments, extends, in short, parallel fasciculi, from the border of one bone to that of the other, and is characterised solely by the presence of numerous, short, unequal-sized, usually elongated nuclei. This *sutural ligament*, as it may be termed, is very evident as long as the cranial bones are still growing, at the same time, that it is softer and differently constituted (*vide* infra). As the growth of the cranium approaches its completion, this tissue gradually disappears, becomes firmer, and, in old age, seems, in many places, especially on the inner part of the sutures, and even before their complete obliteration, to be entirely removed.

2. *Connection* by *ligament*, *syndesmosis*, is effected by means of *fibrous* and *elastic ligaments*. The *fibrous ligaments*, constituting the majority of the ligaments, are white and glistening, corresponding in their structure, partly with the aponeuroses and ligaments of the muscles, and partly with the true tendons.

Elastic ligaments (fig. 121), are, the *ligamenta flava*, between the arches of the vertebræ, and the *ligamentum nuchæ*, which, however, is not nearly so well developed in man, as in some others of the Mammalia. The *ligamenta flava* are yellowish,

highly elastic, strong ligaments, the elastic elements of which, in the form of roundish polygonal fibres, 0·0015—0·004‴ thick, united into a dense network, run parallel with the long axis of the vertebral column, and give the longitudinal, fibrillar aspect to the ligaments. Between these fibres, which are *not collected either into fasciculi or lamellæ*, but are continuously connected throughout the entire thickness of each yellow ligament, there is interposed some connective tissue, upon the whole in small quantity, but demonstrable in every preparation, and occurring in the form of lax undulating fasciculi, which are arranged parallel with the principal direction of the elastic fibres. According to Todd and Bowman (p. 72), the stylo-hyoid, and internal lateral ligament of the lower jaw, are, also, chiefly composed of strong elastic fibres.

Fig. 121.

3. By *cartilage, synchondrosis*. This mode of connection is effected either by cartilage alone, or associated with fibro-cartilaginous and fibrous tissue. The former condition is observed in the adult, only between the ribs and sternum, where, however, properly speaking, a true *synchondrosis* exists only in the case of the first rib, the rest, from the second to the seventh, being connected with the sternum at the anterior

Fig. 121. *A*, transverse section through a portion of the *ligamentum nuchæ* of the Ox, × 350 diam., and treated with soda; *a*, connective tissue, apparently homogeneous; *b*, transverse section of the elastic fibres (0·004—0·01‴ in diameter). *B*, elastic fibres; *a*, from a human *lig. subflavum*, together with some connective tissue, *b*, between them; × 450 diam.

extremity by articulations; whilst the false ribs are either free at the extremity, or are incurved one beneath the other. In the *symphysis pubis*, sacro-iliac synchondrosis, and the junctions of the bodies of the *vertebræ*, the surfaces of the bones are covered immediately by a layer of true cartilage, which, in the two former situations, is directly connected with the opposite layer, and in the latter by means of a fibro-cartilaginous tissue, and is externally encircled by fibro-cartilaginous, and fibrous, concentric layers. In the two former of these instances, there is, not unfrequently, a cavity in the interior of the connecting substance, so that the sacro-iliac synchondrosis, in particular, may also be regarded as a sort of articulation (Zaglas).

[The intervertebral ligaments, or ligamentous discs, of the bodies of the vertebræ, consist, 1, of exterior concentric layers of fibro-cartilage, and whitish connective tissue; 2, of a central, principally fibro-cartilaginous substance; and, 3, of two cartilaginous layers applied immediately upon the bones.

The *concentric lamellæ* consist of alternate layers of connective tissue and of fibro-cartilage, which latter, even in fresh transverse sections, may be recognised as dull yellow streaks, which become hard and transparent in water. The fibro-cartilage, on microscopic examination, presents minute, elongated cartilage cells, disposed serially in a fibrous tissue, differing from connective tissue in its greater rigidity, the absence of distinct fibrils, its great resistance to alkalies and acetic acid, and the total absence of elastic fibres.

The whitish layers of the outer laminæ, although their fibrils are rather more rigid than those of the common ligaments and tendons, are less easily separated, and present but few fusiform cells, and frequently no elastic fibres whatever among them, must nevertheless, at present, be regarded as composed of connective tissue. These laminæ are from $\frac{1}{3}$ to $\frac{3}{4}'''$ and more in thickness, and form entire circles or segments of such, which, alternating with the somewhat thinner, and also frequently incomplete, rings of fibro-cartilage, with which they are closely connected, together with the latter constitute the larger half of the intervertebral ligaments. The general direction of the fibres of both sets of laminæ is

from above to below. They are, however, invariably oblique, so that those of the different layers cross each other. Besides which, it must be remarked, that the individual layers themselves also exhibit a more or less distinctly foliated structure, constituted in such a manner that the fine lamellæ, in the portions composed of connective tissue, observe the same direction as the layers themselves, whilst in the fibro-cartilaginous portions they are disposed more in the direction of the radius of the ligamentous disc.

The softer central substance of the intervertebral ligaments, or the gelatinous nucleus of authors, does not differ, essentially, from the portions above described; for, even in this situation, layers of connective tissue occur, although they gradually diminish in proportion to the fibro-cartilage, and are less distinctly defined. The nearer we approach the centre, the less evident is any trace of an alternation of different layers, and of a concentric arrangement of them; the whole becomes transparent, soft, and, finally, almost homogeneous. The microscope shows the predominance of fibro-cartilage, with large cells (0·012—0·024‴), frequently one within the other (fig. 122); the uniformly thickened walls of which, composed of concentric layers, often enclose merely a minute cavity, with a shrunken nucleus; and besides these, smaller cells frequently in process of dissolution, isolated or aggregated together; and, lastly, an indistinctly fibrous or granular matrix, not unfrequently observed in a state of disintegration, and a considerable quantity of fluid contained in larger or smaller areolar spaces in it. The more central portions of this fibrous substance gradually pass into a thin, hard, yel-

Fig. 122.

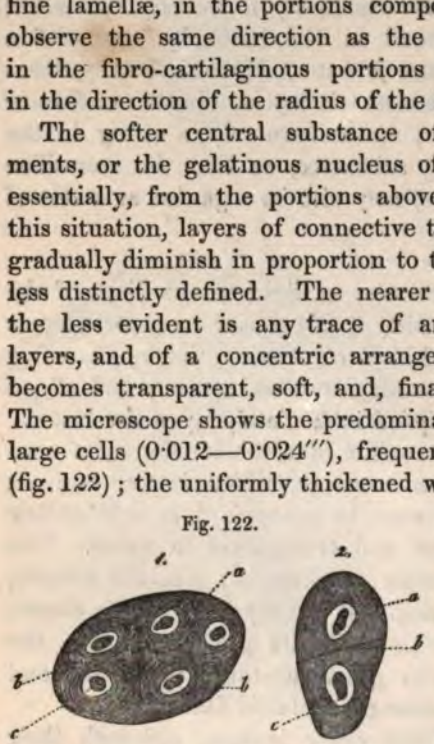


Fig. 122. Cells from the gelatinous nucleus of the *lig. intervertebralia:* 1, large parent cell, *a*, with a septum derived from two secondary cells of the first generation, and five secondary cells, *b*, of the second generation; with concentrically thickened walls and shrunken nuclei, *c*, in the small cell cavities: 2, parent cells, *a*, with two secondary cells, separated by a delicate septum, *b*, and which, with uniformly thickened walls, contain a minute cavity and shrunken nucleus, *c*.

lowish lamella of true *cartilage,* with thickened cells, not unfrequently beset with calcareous particles, which adheres to the bone not unlike an articular cartilage, though less firmly. More externally we find a cartilaginous substance, in the form of isolated minute, discoid, plates or particles, which appear to be in more immediate connection with the fibro-cartilaginous portions, and between these a connective tissue, with scattered cartilage-cells, as in the insertions of the tendons into the bones (*vide* § 81). The more exterior portions of the surfaces of the bodies of the vertebræ, corresponding to these parts of the discoid-ligaments, are, in contradistinction to the more internal portions, as it were porous, after the removal of the ligamentous layer; the medullary cavities or cancelli then being exposed. The pores or cancelli are closed only by the cartilaginous substance of the disc, whilst the fibrous tissue, with its vertical fibres, is firmly connected with the interspaces between them.

Between the *sacrum* and *coccyx,* and the individual coccygeal vertebræ, are interposed the so-called *false inter-vertebral ligaments,* consisting of a more uniform fibrous substance, without any gelatinous nucleus. The separate bones of the *sacrum,* at an early period, have true intervertebral ligaments between them, which afterwards become ossified from without to within, but in such a way, nevertheless, that even in the adult, traces of the ligament may still be perceived in the centre. With respect to the nature of the fibres of the intervertebral ligaments, Donders is inclined, especially from the consideration of their chemical relations, to regard almost all of them, not as connective tissue, but as analogous to the matrix of true cartilage, as is also H. Meyer (p. 300, *et seq.,* and p. 310). This opinion may be correct, as regards the central, nuclear portion, and the fibro-cartilaginous laminæ of the outer portions, but hardly so with respect to the purely fibrous parts of the latter. I believe, moreover, that it is not by chemistry, but by the study of the development of these tissues, that the question will be solved, because, although manifest, visible distinctions exist between the fibrils of connective tissue developed from cells, and the fibrous intercellular substance, viewed from a genetic point of view, chemistry probably is not in a condition to distinguish one from the

other.[1] The intervertebral ligaments are liable to various forms of degeneration; they may become *ossified,* from their cartilaginous lamellæ outwards, the true fibrous substance probably at the same time disappearing; and in this way anchylosis of two vertebræ frequently takes place. They may become *atrophied,* easily broken down, and disintegrated, either in the nuclear portion, or elsewhere in circumscribed spots, into a dirty grumous matter. And lastly, it would appear that although in the normal state, they contain no vessels, vessels may, under certain morbid conditions, be developed in them; at all events, extravasations of blood are not unfrequently met with, most generally close to the bones or in connection with them.

In the *symphysis pubis,* the *cartilaginous layer,* which is thickest in the centre and anteriorly, and connected with the bones by a very uneven surface, consists, at the sides, where it is from $\frac{1}{2}$ to 1''' thick, of true cartilage, with a homogeneous, finely granular matrix, and simple cells, measuring 0·01—0·024'''. In the centre, the matrix is softer and fibrous, and in this situation, (more particularly, it would appear, in the female sex,) there occasionally exists an irregular narrow *cavity,* with uneven walls, and containing a somewhat slimy fluid, originating evidently in a solution of the innermost cartilaginous layers, and of which manifest traces may also be perceived in the cartilaginous substance immediately enclosing it. The outer layers of the symphysis, which, as is well known, are most developed anteriorly and superiorly, do not arise, with the exception of the outermost lamellæ composed of pure connective tissue, directly from the bones, but, properly speaking, unite only the outer portions of the above-described cartilaginous layers, and consist principally of a fibrous substance, to all appearance identical with connective tissue, and occasionally containing cartilage cells.

[1] [In our note on the connective tissue, we have already expressed the views we entertain of the homologies of the elements of cartilage and connective tissue; and we need merely add that we know of no locality in which the transition of the matrix of cartilage into the pseudo-fibrillated collagenous portion of connective tissue is more unmistakeably exhibited, than in the intervertebral cartilages of a young animal, *e. g.*, a kitten. We have, in that note, endeavoured to show that the notion of the existence of any real difference in the development of the fibrillated element in the different forms of connective tissue is unfounded.—Eds.]

The formation of the bone-corpuscles, as they are termed, may be traced perhaps more clearly in the symphysis than anywhere else, except in rachitic bone (fig. 124). For at its osseous borders there are always to be found, either half projecting from, or entirely lodged in, the cartilage, isolated, nucleated bone-corpuscles or cells, with homogeneous, and (from calcareous salts) granular walls, measuring 0·012—0·016''', with respect to which, from their development and from the consideration of the contiguous cartilage-cells, all of which present more or less thickened walls and rudiments of calcareous deposits, not the smallest doubt can be entertained. Well characterised, half and wholly ossified parent cells of the same kind, with two secondary cells, and measuring 0·015—

Fig. 123.

0·03''', up to some including ten or twenty secondary cells, and having a length of 0·05''', may be distinctly noticed in almost every preparation.

The *sacro-iliac synchondrosis* is effected by means of a flattened layer of cartilage, $\frac{3}{4}$—$1\frac{1}{3}'''$ in thickness, which is closely attached to the auricular surfaces of the corresponding bones, between which it is interposed. The cartilage-cells close to the bone are flattened, with their surfaces directed

Fig. 123. Cartilaginous border, towards the cartilage of the *symphysis* in Man, × 350 diam.: *a*, cartilage cells with thickened walls; *b*, the same undergoing ossification; *c*, cells nearly ossified, with homogeneous walls free in the matrix of the cartilage; *d*, similar cells with calcareous granules; *e*, ossified cells at the border of the matrix of the bone containing calcareous granules, and half projecting from it.

towards it, and present beautiful transitionary forms into half and wholly isolated bone-cells, which exist on the border of the bone. In the interior of this cartilaginous layer, according to Zaglas, there is always a narrow cavity, which separates the cartilaginous layers of the two bones completely, or almost completely, from each other. It contains a synovia-like fluid, and is bounded by smooth and even walls, which differ from the rest of the cartilaginous substance in their greater hardness, as well as in their structure. The matrix of these cartilaginous layers, in the direction of the surface, is finely fibrous; the cells are all of large size (as much as 0·035‴), with numerous secondary cells and uncommonly thick walls, so that the cavities, even of the secondary cells, often appear extremely contracted; but they do not exhibit any distinct indication of pore-canals or calcareous deposit.

The *costal cartilages* are invested by a strong *perichondrium*, composed of connective tissue and numerous elastic elements, which commences at the sternal end in connection with the synovial membrane there existing, and at the other is continuous with the periosteum of the ribs. The cartilage, which is in connection with this membrane by a roughened surface, is of considerable firmness although elastic, pale yellow, or in thin sections, exhibiting a transparent blue tint, internally almost always, in certain spots, of a yellowish-white colour, with a silky lustre. Its matrix in the latter situations presents a fibrous structure, and elsewhere a finely granulated aspect. The outermost cells, to the depth of 0·06—0·1‴, are elongated, flattened, parallel to the surface, most usually small (sometimes not more than 0·006‴), but sometimes larger, and filled with one or even many secondary cells, one placed behind the other; more internally, without entirely losing their flattened figure, they are larger (most of them 0·03—0·05‴), oval, and round, and lie with their surfaces towards the ends of the cartilage, and with their long axis for the most part in the direction of the radius of the transverse section of the rib; in many cases, however, they are disposed more irregularly. The largest of these cells (measuring as much as 0·08‴, or even 0·1‴) are found in the fibrous spots, and they, in common with all the interior cells, contain secondary cells, in varying, frequently in very considerable number (as many

as 60, according to Donders). The most remarkable characteristic of the elementary tissue of the costal cartilage, is the large quantity of *fat* contained in it. In the adult, every cell, excepting the most superficial, contains, larger or smaller (from 0·0016—0·008‴), sometimes spherical, sometimes more irregular fat-drops, which frequently so surround the nucleus as entirely to conceal it from view (fig. 124, *a b*), whence it has been assumed, though not quite correctly, that the fat is seated in the latter. The cartilage on the greater cornu of the *os hyoides*, and between the body and the greater cornu, and the inconstant cartilaginous appendage to the styloid process, differ in no respect from costal cartilage, only that the cartilage cells in those instances do not always contain large fat-globules.

Fig. 124.

The costal cartilages frequently become *ossified* in old age; but this ossification, as well as the fibrillation of the matrix, must not be regarded as a normal process, nor be placed in the same category with the usual kind of ossification. The ossification is sometimes more limited, sometimes more extensive. In the former case, it does not proceed further than to the incrustation of the cartilage-cells, and of the matrix in which they are lodged, which has become fibrous; in the latter, and frequently also in the former, the ossification is preceded by the formation of hollow spaces in the cartilage, in which is deposited a cartilage-marrow, containing vessels, which are connected, in part with those of the *perichondrium*,

Fig. 124. Cartilage cells of Man, × 350 diam.: *a*, parent cell with three secondary cells containing oil, from a costal cartilage; *b*, two cells from the same situation, in which the globule of oil is surrounded by a pale border; *c*, two cells with thickened walls from the cartilage of the greater cornu of the *os hyoides*, which together with the globule of oil also contain a distinct nucleus.

in part with those of the ribs; and the osseous substance is more that of normal bone, though almost always more opaque, less homogeneous, and with imperfectly formed lacunæ, which frequently contain a calcareous deposit. Under the name of *cartilage-marrow,* are understood the medulla-cells, fat-cells, bundles of connective tissue and vessels, which are presented instead of the detritus, afforded by the disintegration of cartilage, and which may be said to correspond in all respects with those of developing fœtal bone, and may be readily observed in ossifying costal and laryngeal cartilages.

§ 95.

B. Moveable Articulation (*Diarthrosis*).—The articular extremities of the bones, or any other surfaces entering into the formation of a joint, are invariably invested with a thin layer of cartilage, which in the middle of the surfaces covered by it, is of tolerably uniform thickness, gradually thinning as it extends outwardly, and finally terminating with a very abrupt edge. This *articular cartilage* is closely applied to the bone with a rough, hollowed or raised surface, but is not *united* to it by any interposed substance; and, on the opposite surface, it is in most joints usually quite bare, and directed towards the cavity of the articulation. Sometimes, however, it is invested with a special fibrous membrane, *a perichondrium,* which is an immediate prolongation of the periosteum, and extends most generally only over a small portion of the cartilage, gradually ceasing without any defined margin.[1] In some joints (shoulder, hip) the more secure lodgment of the articular head of the bone is ensured by special cartilaginous lips. These are firm, yellowish-white, fibrous rings, attached, at the

[1] [Reichert, who has paid particular attention to the question of the existence of an epithelium upon the articular cartilages, says, that in the fœtal condition of Man and the domestic Mammalia, an epithelium exists over the whole surface of the synovial capsules, and, on the articular cartilage, lies in immediate contact with its substance. It resembles the epithelium of the vessels. In adults, on the other hand, he could discover an epithelium only on those parts of the articular capsules which are not subject to friction; and here it had the same appearance as in the fœtal condition. It was wanting upon the articular cartilages and their immediate neighbourhood; but it was not uncommon to meet with fine desquamated flakes of cartilage in the synovia, which fell readily into folds, and thus resembled a fibro-cartilaginous tissue (Bericht, Müller's 'Archiv,' 1849, p. 16).—Eds.]

border of the articular cartilage by a wider basis, immediately to the bone or partly to the cartilage. They thin off to an acute edge, and for the most part free and uncovered by the synovial membrane, or any epithelium, project into the articulation, being exteriorly in relation with the periosteum and synovial capsule.

As regards the intimate structure of the parts just described, the articular cartilage, on completely formed bones (fig. 125), and under normal conditions, presents throughout, a finely granular, in part almost homogeneous matrix, in which are lodged delicate cartilage-cells, which towards the surface of the cartilage are numerous and flattened, and lie parallel to it; more deeply they are oval or rounded, more rare, and disposed in various directions; and lastly, close to the bone they are elongated, and placed vertically with respect to the surface of the bone. These cells all have distinct walls, easily distinguished from the matrix by the use of acetic acid, clear, frequently granular contents, containing, however, but little fat, and a vesicular nucleus. They occur either isolated or in groups, and present very frequently two, four or even more secondary cells, which in the flat cells are placed close together, and in the elongated are disposed in rows. On the condyle of the lower jaw, as on the corresponding surface of the temporal

Fig. 125.

Fig. 125. Articular cartilage of a human metacarpal bone, cut perpendicularly, × 90 diam.: *a*, most superficial, flattened cartilage cells; *b*, middle rounded cells; *c*, innermost cells, disposed perpendicularly in small rows; *d*, outermost layer of the bone with ossified fibrous matrix and thick-walled cartilage cells, in this instance appearing dark from their containing air; *e*, true bone-substance; *f*, ends of the cancelli of the apophysis; *g*, one of the cancelli.

bone, until the bone is completely formed, there is a thick layer of very distinctly marked cartilage-cells, covered, towards the cavity of the articulation, by a layer of connective tissue. This cartilaginous layer disappears by degrees, as the bone approaches its completion, and at last there remains beneath the layer of connective tissue, now become both relatively and absolutely thicker, merely an excessively thin and transparent lamina, the elements of which, although morphologically not true bone-cells, nor as yet ossified, still seem to resemble the latter more closely than cartilage-cells.

The cartilaginous lips of the joints consist principally of connective tissue, always containing, however, isolated cartilage-cells of a roundish or elongated form, with a moderately thick membrane, distinct nucleus, and occasionally fat-granules. I have not as yet noticed parent cells in this situation, whilst cells of the kind already described in the muscular system (§ 82), arranged in series, are not unfrequently met with, and might perhaps be regarded as cartilage-cells, although their nuclei exhibit the most evident indications of a transition into nuclear fibres. The articular cartilages, moreover, during their development, which will be entered into more particularly afterwards, have no nerves or vessels, as is the case also with the cartilaginous lips.

[The condition of the bone beneath the articular cartilages, requires special notice. It consists, in almost all joints, in immediate contiguity with the cartilage, of a layer of *incompletely formed bone-substance*, and, more internally, of that tissue in its usual form (fig. 125). The layer in question, which is 0·04—0·16‴, or on the average 0·12‴ thick, is composed of a yellowish, mostly fibrous, hard, and truly ossified matrix, containing, however, not a trace of Haversian canals or medullary cavities, nor of any perfectly formed lacunæ; instead of which it presents roundish or elongated corpuscles, aggregated into little masses or rows, the larger of which are 0·016—0·024″ in length, and 0·006—0·008‴ in breadth, and the smaller 0·006—0·008‴ in length, and 0·004—0·005‴ in breadth, which give thin sections of the bone a perfectly opaque aspect, and consequently might

be regarded as bone-corpuscles (lacunæ) filled with calcareous particles, as which they have lately been considered by H. Meyer (l. c., p. 325, 326). By the addition of spirit of turpentine, which, however, penetrates with difficulty, this error is dissipated, and it is found, that as in the case of the *lacunæ* of dried bone, the opaque aspect is due only to the air contained in them, and that the bodies in question are nothing more than thick-walled cartilage-cells, retaining their contents (fat, nuclei), presenting occasionally indications of canaliculi, and perhaps also partly calcified; in other words, that they are undeveloped lacunæ. The layer in which these cells are lodged, and which, towards the cartilage, is bounded by a straight line, occasionally dark from calcareous particles, and towards the true bone by a sinuous contour, in which the limits, as it were, of the individual lacunæ are distinguishable, is not found either exclusively in bones not yet fully formed, as Gerlach believes, nor only at a more advanced age (from 30 upwards, and particularly in old men), as H. Meyer states, but, at all events as far as my observation extends, at all ages, from the complete development of the bone upwards, invariably in every articulation, except that of the lower jaw and those on the *os hyoides*.[1]

The articular cartilage on the head of the *femur*, in a man 25 years old, measured $1—1\frac{1}{4}'''$ in thickness; on the condyles in the middle, $1\frac{1}{4}'''$; on the margin, $\frac{3}{4}—1'''$; in the *fovea patellæ*, $1\frac{1}{2}—1\frac{3}{4}'''$; in the middle of the condyles of the tibia, $1\frac{1}{2}'''$; at the borders, $\frac{1}{2}—\frac{3}{4}'''$; in the middle of the patella, $1\frac{1}{2}—1\frac{3}{4}'''$; in the glenoid cavity of the tibia, $\frac{1}{2}—\frac{3}{4}'''$; on the body of the *astragalus*, on the upper side, $\frac{2}{5}'''$, on the under, $\frac{1}{2}'''$, on its head, $\frac{2}{5}'''$; at the base of the first metatarsal bone, $\frac{1}{3}—\frac{1}{2}'''$, on its head $\frac{1}{3}'''$; on the inner cuneiform bone, in front, $\frac{1}{3}—\frac{1}{2}'''$, behind, $\frac{1}{2}—\frac{3}{4}'''$. In the fœtus, about the middle period of uterine life, the vessels of the synovial membrane, according to Toynbee ('Phil. Transact.,' 1841), extend much further upon the articular cartilage; of which fact, however, I have been unable to satisfy myself in the *humerus* of a five or six month fœtus, or in new-born infants. In pathological states endo-

[1] [This peculiarity of the bone beneath the articular cartilages was first pointed out by Dr. Sharpey (Quain and Sharpey, 5th ed., p. clviii); and is particularly described by Tomes and De Morgan, l. c., pp. 10, 11.—Eds.]

genous cell-formation is met with in an unusual degree of perfection, and more especially in all kinds of articular cartilages; in which the parent cells, frequently of very considerable size, with one or two generations of secondary cells, and also containing fat, lie tolerably free in the fibrous matrix, and admit of being readily isolated, (*vide* also Ecker in Roser and Wunderlich's 'Archiv,' vol. II, 1843, p. 345). In the adult, the articular cartilages are non-vascular, although the vessels of the synovial membrane, at their border, often advance to some distance over them. What Liston (' Med. Chir. Transact.,' 1840, pp. 93-4) describes as " vessels in the articular cartilage of several diseased joints, and as running straight in parallel lines from the injected membrane of the bone into the cartilage, and as joining at their further extremities in that tissue, thus forming long loops," were certainly nothing more than the normal vessels of cartilage, which (*vide infra*) may be very beautifully displayed even in individuals 18 years old. There cannot, therefore, be any question of inflammation of the cartilages in the adult, though they doubtless suffer in morbid conditions of the bones upon which they rest, or in inflammation of the synovial membrane. They frequently assume a fibrous structure, a change which is often attended with a simultaneous increase in thickness, Cruveilhier, (' Dict. de Méd. et Chir. prat.' III, 514) having noticed fibres of this kind as much as 6‴ in length, thus far exceeding the normal thickness of articular cartilage. They sometimes wear away rapidly, or even disappear altogether (in suppuration in the bone or in the articulation), so that the surface of the bone is left exposed; they also undergo partial losses of substance; when they exhibit ulcerous excavations, which may penetrate to the bone, or commence on the osteal surface of the cartilage.]

§ 96.

The *articular capsules* (*capsulæ s. membranæ synoviales*) are not closed capsules, but short, wide tubular sacs, which are attached by two open ends to the borders of the articular surfaces of the bones, and thus connect them together. They are essentially more or less delicate, transparent membranes, but are in many situations so closely and completely invested externally by

fibrous layers—the fibrous capsules as they are termed,—as on cursory inspection to present the aspect of tolerably tough capsules. These fibrous coats are met with especially in situations where the articulation is either wholly unprotected, or but thinly covered by soft parts, or where a very firm connection is required (as in the hip-joint); they are absent for the most part, or are undeveloped, where muscles, tendons, and ligaments rest upon the articulation, or where, for special purposes, the synovial membrane is exposed to more considerable movements (as in the knee and elbow).

The relation of the articular capsules to the bones and articular cartilages, more precisely described, is as follows (fig. 126):—The articular capsule is attached, either simply to the border of the cartilaginous surface, extending thence directly to the other bone (*patella, amphiarthroses*); or it may, in the first place, besides the border of the cartilage, also invest a larger or smaller extent of surface of the bone itself, and then pass to the second bone, with which it is connected in the one way or the other. In either of these cases the synovial membrane does not adhere immediately to the hard tissues subjacent to it, but is more or less closely connected with the *periosteum* and *perichondrium*, ultimately ceasing without any distinct margin, not far from the border of the articular cartilage, with the perichondrium of which it is inseparably united.

Fig. 126.

With respect to the intimate structure of these tissues, the synovial membranes, distinct from the fibrous capsules, as they are termed, which possess in all respects the structure of fibrous ligaments, consist:—1. of a layer of connective tissue, with not very numerous vessels and nerves; and 2. of an *epithelium*. The latter is composed of from one to four layers of large tesselated cells, measuring 0·005—0·008‴, with

Fig. 126. Diagram of a transverse section of a phalangeal articulation, partly after Arnold: *a*, bones; *b*, articular cartilage; *c*, *periosteum* continuous with the *perichondrium* of the articular cartilage; *d*, synovial membrane at the edge of the cartilage, connected at first with the perichondrium; *e*, its *epithelium*.

roundish nuclei of 0·002—0·003‴. The former, in its innermost part, is constituted of a layer of parallel fasciculi, with indistinct fibrils and elongated nuclei or fine elastic filaments; more externally of decussating bundles, with a fine elastic network, occasionally also of a network of bundles of connective tissue of very various thickness, with winding elastic fibres, exactly as in the arachnoid. Not unfrequently, common fat-cells occur, dispersed here and there in the meshes of the connective tissue, although upon the whole very rarely; and also a few scattered cartilage-cells, with tolerably thick, opaque walls, and a distinct nucleus. The synovial membranes possess neither glands nor papillæ, whilst they present large *adipose masses* (*plicæ adiposæ*) and *vascular processes* (*plicæ vasculosæ, plicæ synoviales, ligamenta mucosa*, Autor.). The former, at one time erroneously termed "Haversian glands," are found principally in the hip- and knee-joints, in the form of yellow or yellowish-red, soft processes or folds, and consist simply of large collections of fat-cells in vascular portions of the synovial membrane. The latter are met with in almost every joint, constituting, provided that the blood-vessels are filled, red, flattened projections of the synovial membrane, with an indented and plicated margin, and furnished with minute processes. These folds are usually placed close to the junction of the synovial membrane with the cartilage, upon which they lie flat, thus forming, in many cases, a sort of coronal around it; in others they are more isolated, and placed in other parts of the articulation. In their structure, they differ from the rest of the synovial membrane, principally in their great vascularity, consisting as they do of little else than minute arteries and veins, and delicate capillaries forming wavy loops at the edge of the processes, and consequently they are very similar to the choroid plexuses in the ventricles of the brain. Besides the vessels, they present a matrix of, frequently, distinctly fibrous, connective tissue, the usual *epithelium* of the synovial membrane, occasionally solitary or numerous fat-cells, and, more rarely, isolated cartilage-cells. At the edge, they are almost invariably furnished with minute, foliated, conical, membranous processes of the most extraordinary forms (often resembling the stems of a *cactus*), which also frequently contain vessels, but are for the most part constituted merely of an axis of indistinctly fibrous

connective tissue, with occasional cartilage-cells, and an *epithelium*, very thick in places. The smaller ones frequently consist even of nothing but *epithelium*, or of little else than connective tissue.

Fig. 127.

In many joints there are firm, whitish-yellow fibrous plates, the so-termed interarticular cartilages or ligaments which, either projecting in pairs from the synovial capsule, are interposed between the bones constituting the articulation (knee), or form a single diaphragm transversely across the joint (articulations of the jaw, clavicle, *sternum*, and wrist). These processes consist of a firm, fibrous tissue, the fibres of which, usually cross each other in various directions, and are in all respects closely allied to connective tissue, but presenting less distinct fibrils; and besides this, of cartilage-cells and fine elastic fibres. The cartilage-cells, in the most superficial layers, are more solitary, in the deeper, disposed more in *rows* and smaller, ultimately being replaced by fine elastic fibres, a certain number of which, at all events, appear to originate from cells resembling the cartilage-cells. The interarticular ligaments, which, from what has been said respecting them, must be enumerated among the fibro-cartilages, are not covered by synovial membrane, though they probably have an epithelial investment at the attached border, but only for a small

Fig. 127. From the synovial membrane of a phalangeal articulation: *A*, two non-vascular appendages of the synovial processes, × 250 diam.; *a*, connective tissue in its axis; *b*, *epithelium* (in the peduncle of the larger process not distinctly cellular) continuous with that on the free borders of the process; *c*, *d*, cartilage cells: *B*, four cells from the *epithelium* of the synovial membrane of the knee, one with two nuclei, × 350 diam.

extent,—never over the entire surface. The *articular ligaments*, with the exception of the softer *ligamentum teres*, are composed of the same firm connective tissue (in the costal ligaments containing cartilage-cells), as that of which the tendons and the fibrous ligaments, elsewhere, are constituted. The internal ligaments (*lig. cruciatæ*), however, present softer connective tissue, containing vessels, and covered with epithelium.

Fig. 128.

Within the synovial capsules, is contained, in small quantity, a clear yellowish fluid, which may be drawn out into threads,—the *synovia*,—and which, in its chemical composition, appears very closely to resemble mucus, and particularly in its containing *mucin* in solution. Examined under the microscope, in its normal condition, this secretion exhibits nothing worthy of much remark, consisting simply of fluid which is rendered turbid by acetic acid, and very frequently contains epithelial cells, which have often undergone a fatty metamorphosis, nuclei of such cells, and fat globules; under conditions, not quite normal, it may also contain, blood- and lymph-corpuscles, detached portions of the synovial processes of the articular cartilage, and a structureless gelatinous substance.

[The normal, healthy *synovia*, which in the Ox, according to Frerichs (Wagn. 'Handb.' III, 1), contains 94·8 water, 0·5 mucus and epithelium, 0·07 fat, 3·5 albumen and extractive matter, and 0·9 salts, is a secretion, not having essentially any formed elements in it, which simply exudes from the vessels of the synovial membrane with the intermediation of the epithelium; and, in fact, from all its vascular processes, which are destined as it were for this special function, and always exist at the border of a cartilage requiring a lubricating covering. The non-vascular appendages of these processes give

Fig. 128. From the falciform ligament of the knee: *a*, a filament of connective tissue with oval cells disposed in a series, and resembling cartilage cells; *b*, a similar filament with more elongated cells and nuclei.

origin to the "loose cartilages," as they are termed; they do this by their increasing in size and solidity, and becoming detached from the vascular folds. These bodies are also met with, in mucous bursæ and the sheaths of tendons, which are also furnished with vascular folds (*vid. sup.* § 82); they consist of connective tissue with elongated nuclei, coated with epithelium, and, though not always, contain a variable number of scattered fat- and true cartilage-cells; and they are not developed externally to the synovial membrane, but from an outgrowth of that membrane itself. Similar solid bodies, moreover, may probably be produced in other ways; Bidder ('Zeitsch. f. rat. Medicin.,' vol. iii, p. 99, *et seq.*) at all events, and Virchow ('Med. Zeitung,' 1846, Nos. 2 and 3) have observed similar bodies presenting no trace of organization. I am inclined, with Virchow, who has actually demonstrated the presence of fibrin in them, to regard them, in many cases, as fibrinous exudations, and in others as solidified deposits from the synovia, which latter supposition is supported by the frequent occurrence of curdy, more or less consistent, structureless masses, evidently inspissated synovia, in the tendinous sheaths of the hand. Portions of bone, also, detached from outgrowths at the circumference of the articular ends of the bones, may find their way into the interior of the articulation. The *plicæ adiposæ* have perhaps less to do with the formation of the synovia, than with the mechanism of the joint, serving the purpose of filling up hollows.]

§ 97.

Physical and chemical properties of the Bones, and their accessory Organs.—The bones are composed, besides a small quantity of water (3—7%, according to Stark in the compact substance), and fat (2—3% Bibra), principally of a substance affording gelatine, and of inorganic elements. The latter, in the adult, constitute two thirds (68·82 Bibra) of dry bone, and are nearly all left when the bone is calcined; in which case, if due care be taken, the bone completely retains its external aspect, although it may be readily reduced to a white, opaque, friable, heavy powder, the so-termed "bone earth." This consists chiefly of 57—59% basic phosphate of lime (according to Heintz, 3 atoms base, 1 atom acid), of carbonate of lime (7—8%) and

traces of fluate of lime, phosphate of magnesia, silex (traces), and alkaline salts. A small part of the salts of bone is also contained in the walls of the vessels and in the lacunæ, and this part is dissolved in water. The collagenous substance is the so-termed *bone*, *formative*, or *ossifying* cartilage. It is obtained when bone is treated at a low temperature with dilute hydrochloric, or nitric acid, in the form of a soft, flexible, elastic, light-yellowish, cartilaginous, transparent substance, retaining accurately the shape of the bone. This bone-cartilage constitutes about $\frac{1}{3}$ of the dry bone, putrefies when moist, and when dried, may be burnt away, leaving a small quantity of ash. It is dissolved by boiling, and from its combination with water is produced the gelatine, usually to the amount of 3 or 4 times its volume, and which may also be obtained directly by long boiling of the bone in a Papin's digester.

With regard to the mode in which the principal constituent elements of the osseous tissue are combined, it is certain that the bone earth does not exist as a distinct deposit in any of the constituent parts of healthy, fully formed bone, but rather, although in a solid form, only in a very *intimate union* with the tissue. Since both the cartilage and the calcined bone retain the figure of the bone, in all its particulars, independently of each other, there can be no doubt, but that the most intimate union of the two substances exists throughout the entire bone, which, however, cannot be regarded as a chemical combination, principally for the reason, that the proportional relations between the collagenous substance and the phosphate of lime are very variable; and that, by simple boiling under an increased pressure, the gelatine is separated from the calcareous salts.

The *physical* properties of the bones correspond with their composition. Their hardness, density, and rigidity are due to the earthy, whilst their elasticity and flexibility depend upon the organic constituents. In the normal bone of the adult, the two principal constituents are united in such proportions, that the bones, together with considerable hardness and rigidity, have a certain degree of elasticity, though slight, so that they possess a considerable resisting power, and are broken, though not very readily, by the application of greater mechanical

force. At an earlier age, when the cartilage is in greater relative proportion, the hardness of the bones is much less, their sustaining power consequently less considerable, and they are more liable to be bent; whilst on the other hand, owing to their greater elasticity, they are much less liable to be broken. This is the case in a much higher degree in *rachitis*, in which morbid condition, the organic constituents amount to from 70 to 80 per cent. A condition the reverse of this is observed in old age, when the bones, though certainly harder, are more brittle, and therefore more readily fractured, to which liability, however, the rarefaction of the tissue which takes place in consequence of age, partly contributes. The inflammability of bone depends upon its organic basis, and its capability of resisting putrefaction to the inorganic constituents. The latter being so intimately combined with the animal tissues, serve as a protection to them, so that bones from ancient burial places, and those of fossil animals still retain the full proportion of cartilage.

The *true cartilages*, even in the fœtus, contain, in their organic basis, from 50 to 75 per cent. of water, 3 to 4 per cent. of salts (chiefly of soda and carbonate of lime, and also some phosphate of lime and magnesia). The organic basis, has been hitherto supposed to consist entirely of *chondrin*, a substance allied to gelatin, soluble in boiling water and gelatinising as it cools; but it was noticed by Bruns (p. 216), that the matrix and the cells of cartilage were not equally soluble in water, and Mulder and Donders have rendered it probable that the *chondrin*, which had hitherto been investigated, is not a simple substance, and that the cartilages consist of several bodies of different natures, the matrix, and the membranes of the parent cells, their contents, and the secondary cells, of which the first is more soluble in water, potass, and sulphuric acid, than the others.

The fibro-cartilages (cartilages containing connective tissue) have been, as yet, but little investigated. J. Müller, in the interarticular cartilages of the knee of the Sheep, found no chondrin; whilst Donders, on the other hand, met with it in the intervertebral ligaments ('Holl. Beitr.,' p. 264); he did not determine whether they also contained gelatin. According to Virchow, the gelatinous, nuclear portion of these ligaments,

in the new-born child, consists of a substance very nearly allied to that of "colloid" (Wurzb. 'Verhandl.,' II, 283). The ligaments have the same chemical composition as the tendons.

§ 98.

Vessels of the Bones and their accessory Organs.—A. Blood-vessels. The *periosteum*, besides the numerous vessels passing to the bone by which it is traversed, presents in its outer layer, composed of connective tissue, a tolerably close network of minute capillaries (0·005‴). The blood-vessels of the *bone* itself are very numerous, as may be seen in injected specimens, and also in recent bone full of blood. In the *long bones*, the marrow and the spongy substance of the articular ends are supplied by particular vessels, as is also the compact substance of the shaft. The former, or *vasa nutritia*, enter the bone through large special canals, one or two of which are found in the *diaphyses*, and many in the *apophyses*. These vessels, with the exception of a few twigs given off to the innermost Haversian canals of the compact substance, and which possess all the tunics proper to the vessels elsewhere (even to the muscular), ramify in the marrow, where they form a true capillary plexus—the vessels in which vary in size from 0·004‴ to 0·0052‴. The vessels of the *compact substance* arise, in great part, from those of the *periosteum*, very soon lose the muscular coat, and form, in the Haversian canals, which they either occupy by themselves, or together with some medullary substance, a network of wide canals, which from their structure, can only in the most trifling extent be referred to the capillary system, most of them possessing a layer of connective tissue and an epithelium, and as it is only in the larger canals that fine capillaries co-exist with the main vessel. The *venous blood* is returned from all the long bones, in three ways:—1. by a large vein accompanying the nutritious artery, the ramifications of which it follows; 2. by numerous large and small veins at the articular extremities; and, 3. lastly, by many small veins, which arise independently of each other from the compact substance of the *diaphyses*, in which their roots, as is correctly stated by Todd and Bowman, occupy the wider spaces and sinuses, or pouch-like excavations, which are very evident even in sections of bone.

All the vessels of bone,—the medullary vessels of the *apophyses* and of the *diaphyses*, as well as the vessels of the compact substance,—communicate in a multiplicity of ways, so that the vascular system throughout the entire bone constitutes a continuous whole, in which it is possible for the blood from any one part to reach every other part; for it was observed by Bichat ('Anat. Général.,' 1812, III, p. 37), in an injected *tibia*, the nutritious artery of which was obliterated, that the bifurcation of the vessel in the medullary canal was well injected, and that the nutrition of the marrow was evidently unaffected.

In the *short bones*, the blood-vessels present pretty nearly the same conditions as they do in the *apophyses* of the long bones; the arteries and veins of larger and smaller size entering and quitting the bone at numerous points on the surface, and sometimes, as in the posterior aspect of the bodies of the *vertebræ*, in very large trunks,—the *venæ basi-vertebrales* of Breschet, furnishing a capillary plexus to the medulla, and also penetrating into the few Haversian canals of these bones.

In the *flat bones*, such as the *scapula* and *os innominatum*, there are distinct nutritious foramina for the larger arteries and veins; the compact substance receiving finer vessels from the *periosteum*, and the spongy substance being supplied by numerous and even large vessels, as in the neighbourhood of the articular cavities. In the flat *cranial bones*, the arteries, for the most part, enter both the cortical and spongy substance from without, on both surfaces, presenting the usual conditions, whilst the *venæ diploeticæ*, as they are termed, have only their extremities free in the medulla, as in other bones, their trunks, and larger and smaller branches running independently and generally unassociated with medullary substance in large, arborescent, special channels, the so-termed "canals of Breschet," which open at determinate points with large apertures (*emissaria Santorini*), and communicate freely with the veins of the *dura mater*, with respect to which relations, however, works on special anatomy must be consulted. The size and number of the veins in the cranial bones, is, moreover, extremely variable, and they are constantly becoming obliterated, particularly in old age, concomitantly with the frequent diminution of the *diploe*, on which account also the venous

canals and their openings (*emissaria*) are of such variable dimensions.

The articular and other cartilages of the osseous system, even the fibro-cartilages, in the adult, normally contain no vessels at all, except those of the *perichondrium*, which however in this respect is far inferior to the *periosteum*. But it may happen, that as in the costal cartilages in the middle period of life and afterwards, vessels make their appearance, in which case partial ossification frequently either precedes or follows. The *fibrous ligaments* are poorly supplied with vessels, and particularly the *elastic ligaments*, and in this respect may be arranged with the tendons, whilst the *synovial membranes* are characterised by the considerable number of their blood-vessels. The above-described synovial folds are especially rich in this respect, as is also the synovial membrane itself, which, every where beneath the epithelium, contains a pretty close plexus of canals, from 0·004—0·01 in diameter.

B. Lymphatics in bone, have been described by some older and more recent authors (vid. Mikrosk. 'Anat.,' II, 1, 336), but their existence is still not the less doubtful, and I have in vain endeavoured to find such vessels. With respect to the other parts of the osseous system, the only question can be, as to whether the *periosteum* and articular capsules possess lymphatics. In the former, they have not yet been observed, whilst in the latter their existence has been asserted by several authors, Cruveilhier, for example. It must be confessed, however, that it has not been by any means proved that they arise in these structures, at all events it appears to me to be very doubtful, whether the synovial membranes themselves contain vessels of this kind, whilst it is perhaps certain that lymphatics do exist in the loose connective tissue surrounding the articular capsules, and between them and the periosteum of the apophyses, particularly at the knee.

§ 99.

Nerves of the osseous System.—The *periosteum* is abundantly supplied with nerves, the majority of which, however, do not belong properly to it, but to the bone (*vid. infra*). With respect to the proper periosteal nerves, it appears that their number, on the whole, is not considerable, so that even

in some places they may be entirely absent, as in the neck of the *femur*, and beneath certain muscles (*glutæus minimus, peronæi*, &c.); but there are perhaps but few bones in which they do not exist in one part or another. These nerves lie in the same layer as the vessels, sometimes along the larger branches, sometimes by themselves, arising, at all events in part, from the larger nerves of the bone itself, and are manifestly distributed over considerable spaces, although their ramifications and anastomoses are scanty. In the larger trunks of these nerves the primitive fibres measure, most generally 0·002—0·004‴, though their size gradually lessens, partly owing to actual divisions, which I have seen with the utmost distinctness in the *periosteum* of the *fossæ infra-spinata*, and *iliaca* in man, and J. N. Czermák in that of the frontal bone in the Dog; and in part by a gradual attenuation, to a diameter of 0·0012—0·0016‴, many, and perhaps all, terminating with free extremities. On the articular ends of many bones, such as those of the elbow, knee, and knuckle-joints, I have noticed the nerves to be more abundant than elsewhere, ramifying and anastomosing in the vascular connective tissue covering the *periosteum*, and following principally the course of the blood-vessels; but in these situations, divisions and terminations of the primitive fibres did not come under my observation.

The *nerves of the bone* itself, which, with the exception perhaps of the *ossicula auditûs* and sesamoid bones, are universally present, do not exhibit exactly the same conditions in all bones. In the larger *cylindrical bones*, they penetrate, in company with the nutrient vessels, in the form of one, or where two nutrient foramina exist, of two, pretty considerable trunks (measuring as much as 0·16‴) visible to the naked eye, directly into the medullary cavity, and are there distributed in the medulla, following the course of the vessels, though not always in apposition with them, towards the *apophyses*, and forming multifarious ramifications, but, at least as far as I have seen, only few anastomoses. In the second place, all these bones also present, in the *apophyses*, numerous finer nerves, accompanying the equally numerous blood-vessels directly into the spongy substance, and ramifying in the medulla; and thirdly, extremely delicate filaments are sent

even into the compact substance of the *diaphyses*, in company with the minute arteries by which it is penetrated. There can be no doubt that these filaments are distributed in the compact substance, although I have never succeeded in finding them within it. The *smaller cylindrical bones of the hand and foot* present the same conditions with respect to their nerves as the larger ones, except that in them, on account of the undeveloped condition of the medullary cavities, the numerous nerves are not so regularly divided into apophysal and diaphysal.

Of the *short bones*, I have found the *vertebræ* to be the most abundantly supplied with nerves, and especially their bodies. The nerves enter posteriorly in company with the arteries and veins (*venæ basi-vertebrales*), as well as anteriorly and on the sides, together with the vessels, and are distributed in the marrow of the spongy substance. In the *astragalus* also, *calcaneum, os naviculare, cuboideum,* and *cuneiforme internum,* I have noticed, in the larger, several, and in the smaller, at least one nervous filament.

In the *scapula* and *os innominatum*, the nerves are very numerous, entering these bones chiefly at the points before indicated, with the larger vessels, sometimes on the expanded portion, sometimes in the neighbourhood of the articular cavities. In the *sternum* also, and in the flat cranial bones, the existence of nerves is demonstrated without difficulty. In the latter, I have observed, even in the new-born infant, in the occipital and parietal bones, nerves entering through the *foramina emissaria*, which at this period also contain an artery; and in the adult, there are found in the parietal, frontal, and occipital bones, although rarely, yet occasionally, microscopic filaments on the smaller arteries, which enter the compact substance from without, and probably penetrate as far as the *diploë*.

From these observations, together with those of Kobelt, Beck, Engel, Luschka, &c., there can be no doubt that the bones are richly supplied with nerves. With respect to the origin of these nerves, they have already been traced by previous observers to the cerebral and spinal nerves, as for instance the nerves of the *diaphyses* of the *femur, tibia,* and *humerus*, to the *nn. cruralis, tibialis, ischiaticus,* and *perforans Casseri,* as well

as a nerve of the frontal bone to the *n. supraorbitalis*, which observations, as far as they relate to the tibial nerve, have been confirmed by my own, and by those of Luschka in the case of certain of the cranial bones, and of the *vertebræ*. Nevertheless, the *sympathetic* participates in their formation, as Luschka, and before him, Kobelt have observed with respect to the vertebral nerves. Microscopical examination confirms this, inasmuch as the nerves of bone, in their trunks and terminations, resemble in every respect the sensitive branches of the spinal nerves, and contain, in the trunks, one third of fibres, measuring 0·005—0·006‴; two thirds measuring 0·002—0·004‴; in the larger branches the majority of the fibres measure 0·002—0·003‴, but some as much as 0·006‴; and lastly, in the finest ramifications, fibres of not more than 0·0012—0·0016‴. The periosteal nerves, also, which may frequently be seen to be connected with the nerves of the bone, and may be traced to the nerves of the extremity, are derived, probably in the greater proportion, from the spinal nerves, although even in their case, perhaps, some participation of the sympathetic cannot be denied.

How the nerves of bone terminate, I have not observed, and can only remark, that from the nerves in the marrow, extremely delicate branches, composed of neurilemma and one or two fibrils, are ultimately developed; but as to what becomes of these I am ignorant. It is also, perhaps, worthy of notice, that in two situations, before their entrance into the bone, I have observed Pacinian bodies on the nerves; viz. on the diaphysal nerve of the *tibia*, two lines before its entrance into the foramen, I noticed a single body, and two others on the largest nerve of the metatarsal bone of the great toe, also just before it entered the bone.

I have never yet detected nerves in the *ligaments*, in Man (the *ligamentum nuchæ* of the Ox contains some fine nervous twigs, accompanying minute arteries; the twigs measuring 0·004‴, with fine fibres of 0.012—0·0015‴), but have no doubt that they, like the tendons, inasmuch as that they contain vessels, are also furnished with a few scattered nerves. On the other hand, the interosseous membrane of the leg contains filaments derived from the interosseal nerve, which, formed of from one to three fibrils, measuring 0·003—0·004‴,

present distinct ramifications and free terminations of the primitive fibrils. A nerve of 0·03‴, which together with an artery entered the fibrous external part of the *symphysis pubis*, may here be mentioned. With regard to the cartilages, I have as yet noticed only in the cartilage-canals in the *septum narium* of the Calf, together with vessels (arteries), very distinct, fine nervous twigs, measuring 0·006—0·01‴, with fibres of 0·0012—0·0016‴ thick. In the articular capsules numerous nerves exist, although they belong principally to the so-called fibrous capsules, and to the loose connective tissue external to the synovial membrane. In the knee I have seen nerves, even in the true synovial membrane, although in general they are rare, and are most distinct in the large vascular processes, which besides arteries, contain nerves of 0·007—0·008‴, with fine, also dividing filaments of 0·0008—0·002‴. I have also seen in the synovial membrane itself, close to the condyles of the femur, tolerably numerous nerves composed of delicate fibres.

§ 100.

Development of the Bones.—In respect of their development, the bones fall into two groups, viz. into those which are preformed in *a cartilaginous state* (primary bones), and into those which *from a small beginning are developed in a soft blastema* (secondary bones). The former, while yet in the cartilaginous condition, present all their essential parts (diaphyses and apophyses, body, arches and processes, &c.), and as far as their cartilaginous basis is concerned, originate like other cartilages, and continue to grow more or less in the same manner. They afterwards become ossified (in man, all of them) from within to without, transforming a portion of the cartilage completely into bone, so that what was the perichondrium becomes the periosteum, and afterwards attaining their ultimate figure, partly by means of the remaining cartilage, which continuing to grow with them is successively ossified, and partly by means of a soft, ossifying blastema, which is deposited layer upon layer on the inner surface of the periosteum. In the second group, the bone is formed from a very limited, soft, non-cartilaginous basis, and continues to grow at the expense of that substance, which is

continually developed anew, first at the margins only, but afterwards also on the surfaces. When these bones have attained a certain size, the *blastema* out of which they have hitherto been developed may become, partially, cartilaginous, in which case the cartilage stands in the same relation to the bone as it does in the former instance. The greatest part of their formative substance, however, always remains in a soft condition, and from it, without its ever becoming cartilaginous, the principal bulk of the bone is produced.

[Frequently as the development of the osseous tissue has already been discussed, still, in a general point of view, the mode in which the bones, as organs, originate has hitherto been little considered, and I believe that I was the first, in my 'Zootomical Report,' Leipzig, 1849, to establish the principal features of the process, and in my 'Microscopical Anatomy,' II. 1, p. 344, *et seq.*, to trace it in its more particular details. H. Meyer (l. c.) agrees with me in most of the essential points, whilst Robin advances many different views, with which I do not accord, and has to some extent entirely misunderstood my statements.]

§ 101.

The *primary cartilaginous Skeleton* of the human body, although less complete than the subsequent osseous framework, is still sufficiently extensive. We find as portions of it: 1. A complete vertebral column, with as many cartilaginous, as there are afterwards osseous *vertebræ*, with cartilaginous processes, and with intervertebral ligaments. 2. Cartilaginous ribs, and a cartilaginous, entire sternum. 3. Wholly cartilaginous extremities, with as many and similarly formed pieces as there are afterwards bones, with the sole exception of the pelvic cartilages, which constitute a single mass. 4. And lastly, an incomplete cartilaginous cranium. This *primordial cranium*, as it is termed ('Mikrosk. Anat.,' tab. iii, figs. 1—3), forms originally a continuous cartilaginous substance, which corresponds, for the greater part, with the occipital bone (except the upper half of the expanded portion), the sphenoid (except the *lamina externa* of the pterygoid process), the mastoid and petrous portions of the temporal bone, the ethmoid, the inferior turbinated bones,

the *ossicula auditus* and the hyoid bone; but it also presents some cartilaginous portions, which never become ossified, either remaining in the cartilaginous condition during life, or afterwards disappearing; as for instance, Meckel's process, two cartilaginous lamellæ below the nasal bones, a narrow cartilaginous band connecting the styloid process with the *os hyoides*, and two others, one of which extends from the outer part of the *ala parva* laterally to the *lamina cribrosa*, whilst the other stretches upwards and forwards from the cartilaginous, mastoid and petrous portions of the temporal bone. Consequently, in the cartilaginous cranium of man, the vault of the skull is totally wanting, and almost all the lateral portions, as well as nearly all of what afterwards becomes the facial bones; nevertheless, at all events in the true cranium, the parts not formed of cartilage are closed by a fibrous membrane, representing in fact the further development of the soft, primordial, cranial capsule, so that the cranium at this time, though only in part cartilaginous, is yet fully as complete as at an earlier period, and always corresponds to its original soft rudimental form. In other Mammalia, as for instance, in the Pig, the cranium is much more completely cartilaginous ('Mikroskop. Anatomy,' tab. iii, figs. 4, 5.)

[The complete development of the primordial cartilage, considered *histologically*, has not yet been accurately traced in all its stages, either in man or in the mammalia. If we wish, therefore, to obtain anything like a sufficient idea of it, we must at present have recourse in a great measure to the lower Vertebrata. If the cartilage of the spinal column and of the head be examined in the *batrachian larva*, it is readily seen, that they are invariably constituted, while still in the soft state, of the same formative cells with vitelline corpuscles, as all the other organs. Before the development of the external branchiæ, these cartilage-cells present the form of closely approximated spherical cells, 0·007‴ to 0·009‴ in size, with nuclei measuring 0·0045—0·006‴, and filled with the well-known vitelline corpuscles; afterwards, when the branchiæ have made their appearance, the granular contents of the cells begin to disappear, from within to without, whilst the nuclei become more distinct, lying in a clear fluid within them, and at the same time the cells slowly

increase in size. When the branchiæ have disappeared, all the cartilage-cells are already quite transparent, with distinct nuclei and walls, and they now gradually increase to the size of 0·018—0·024‴, and the nuclei to that of 0·005 and 0·007‴; the cells, from their mutual pressure, become polygonal, and constitute one of the most delicate cellular tissues possible. They now also begin to multiply by endogenous cell-formation around portions of the contents (Nägeli), so that in each cell two secondary cells are formed around the two nuclei produced from the original nucleus, and entirely fill it; at the same time they again increase, though very slowly, particularly in certain cartilages of the head, until they attain a size of 0·013—0·018‴, and in some places of not more than 0·006—0 013‴; whilst between them, a thick interstitial substance is formed out of the coalesced walls of the different generations of cells. With respect to man and the mammalia, it can only be stated as a supposition, that the cartilage-cells originate in a modification of the primordial formative cells. This supposition is favoured by the circumstance, that in a human embryo of eight or nine weeks, the outer extremities of which were just developed, they presented scarcely a trace of formed cartilage, the innermost cells of the rudimentary extremities being hardly distinguishable from the outer. They were 0·004—0·006‴ in size, spherical, with greyish granular contents, and indistinct nuclei of 0·003‴, and formed a tissue of some consistence, without any appreciable interstitial substance. The corresponding cells in the embryo of a sheep 6—7‴ in length, were somewhat larger, although the embryo was smaller than the human fœtus above noticed. In this case (fig. 129) they measured, for the most part, 0·006—0·01‴, had distinct walls, nuclei, and clear, aqueous, only slightly granular contents, and were lodged in a scanty homogeneous interstitial substance, so that they were only

Fig. 129.

Fig. 129. Cartilage-cells from the *humerus* of an embryo of the Sheep, 6‴ long: *a*, cells with nucleus and clear contents (two cells retain remains of the earlier thick contents); *b*, cells with consistent contents, without visible nucleus; *c*, intercellular substance.

partially or not at all in contact with each other. The contents of only a very few cells were still in the opaque condition, and these were without any visible nucleus, others exhibited the commencement of transparency from the metamorphosis of their contents. The further development of the cartilage up to the end of fœtal life, except in its ossification, presents these characteristics, viz.: (1.) That the cells, precisely like those in the batrachian larva, continually increase by endogenous cell-formation, whilst precisely as in the same instance, there is no indication whatever afforded, of the *production of cells, independently of those already in existence*; and (2.) That the interstitial substance, which in this case is manifestly formed, for the greater part, independently of the cell membranes, *is always increasing*. With respect to the cells, they are, in the second costal cartilage of a four-month fœtus, according to Harting, 0·0036‴ long, 0·0023‴ wide, and consequently their aggregate bulk pretty nearly corresponds with that of the interstitial substance. In the embryo of the Pig, 3·5‴ long, the space occupied by the nucleated, clear, thin walled cells, is, according to Schwann, thrice as great as that taken up by the interstitial substance. In a five-months' human embryo, I have myself noticed the cartilage cells, 0·003—0·008‴ in diameter, with and without secondary cells, some with, and some without distinct walls, and separated from each other by a perfectly homogeneous substance 0·002—0·005‴ thick. In the new-born child they measure, according to Harting, 0·032—0·028$^{\text{m.m.}}$ in length, and 0·0072$^{\text{m.m.}}$ in breadth, and are three or four times as numerous as in the fœtus at four months; but on the other hand, they occupy considerably less space, proportionally, than the interstitial substance, the bulk constituted by which is more than double that of the cells. After birth, in the non-ossifying cartilages, the interstitial substance and the cells increase in pretty nearly an equal ratio, so that their relative proportions in the adult are about the same as in the infant at birth. In the adult the cells are from 8 to 12 times larger than in the new-born child (Harting), but, according to him, their number is diminished, so that they amount to not more than half of what existed in the child, which is explained upon the supposition of a coalescence of the cells. The numbers given by Harting do not appear to me

to afford sufficient ground for the establishment of his position; and even should it be established, I cannot agree in the explanation offered, not being aware of a single fact in favour of the notion of a coalescence of cartilage cells.] [1]

[1] [We have deferred to this place the remarks we have to make with regard to the structure of cartilage, and its mode of growth; as a just conception upon this subject appears to us to be essentially necessary to a comprehension of the mode of development of Bone,—in fact, we might say, to clear notions upon the structure of the tissues generally; for as we shall show more at length below (Appendix), it was upon the structure of cartilage, and what he supposed to be its similarity to that of vegetable tissue, that Schwann based the whole nomenclature of his cell theory.

Now we may so far anticipate what we shall have to show hereafter, as to premise that Schwann was misled upon two essential points,—the first being the supposition that the histological elements of plants and animals are *primarily independent cells;* the second, the notion that the "nucleus" of the animal, is homologous with the nucleus of the vegetable tissue. It is, we believe, from the inextricable confusion produced by these fundamental mistakes, which have been adopted by almost all Schwann's successors, that one half of the controversies with respect to the structure of cartilage and the process of ossification have arisen. And yet to one who is free from them, nothing can be simpler.

We have already (note p. 30) referred to the structure of fœtal cartilage, but it may here be described more at length. We found the cartilage of the *septum nasi* of a four-months' human fœtus to be composed of a homogeneous, soft matrix, without structure of any kind (fig. 129 *A*, 1, 2), in which lay imbedded, rounded or irregular vesicular bodies, varying in diameter from $\frac{1}{3000}$—$\frac{1}{5000}$th of an inch; the commonest size, however, being $\frac{1}{5000}$—$\frac{1}{2500}$th. These "corpuscles" frequently contained one or more granules, sometimes very small, sometimes larger, and of a distinctly fatty nature; such fatty granules, also, were sometimes to be found in the matrix around the corpuscles.

The cavities in which they lay, were, for the most part, just large enough to contain them, and presented no walls or sharp line of demarcation of any kind from the surrounding substance.

When the corpuscles were as large as $\frac{1}{1800}$th of an inch, they occasionally contained a round body, of rather less than $\frac{1}{5000}$th, as a "nucleus."

The matrix was in some parts pale and indifferent; but where the tissue had taken on its definitely cartilaginous nature, the chondrinous substance into which it was converted refracted the light much more strongly. In this part also, the cavities in which the corpuscles lay, were often of considerably larger dimensions than the latter, and their walls exhibited a sharp, dark line of definition from the surrounding substance, which was often brought out much more strongly by the action of acetic acid. It appeared, in fact, that the conversion into chondrin had not quite reached the inner surface of the cavities, and hence they were chemically and optically distinguished from the surrounding substance.

Now, of course, it matters very little what names are given to these parts, so long as they are used only in one sense. Schwann considered the corpuscles to represent the "nuclei" of plants, and therefore gave them that name. Henle, Reichert

§ 102.

Metamorphoses of the primordial cartilaginous Skeleton. Of the primordial cartilages, one portion undergoes further deve-

Kölliker and nearly all their compatriots, Todd and Bowman, Leidy and Sharpey —follow him. As a consequence, they consider the wall of the cavities to represent the cellulose "cell-wall" in plants; and there has been much controversy as to how much of the matrix of the cartilage results from the union of these "cell-walls," how much from the development of an intercellular substance; a controversy which has extended itself to the determination of the homologies of the elements of every tissue. We must confess, it seems to us that the disputants have been fighting for a shadow.

Fig. 129 *A.*

If, in fact, the youngest cartilage be composed of cells with distinct walls inclosing the corpuscles, of course these cells may be united by an intermediate, "intercellular" substance; and it will be an important question to determine in the further course of development, what arises from the walls and what from the substance which unites them. But if, on the other hand, all this be pure hypothesis; if young cartilage be, as we have said, composed of nothing but a continuous, homogeneous matrix, in which the corpuscles are imbedded, but in which no other structure exists, what becomes of the controversy?

We believe, that not merely will the account we have given, be found to be correct,

Fig. 129 *A.* 1, 2, cartilage from the *septum nasi* of a four-months' human fœtus. 3, 4, 5, 6, cartilage from the extremity of the humerus in a kitten just born: 3, 4, corpuscles in various stages of division; 5, a nucleated corpuscle, free; 6, "jagged" corpuscles near the ossifying surface: 7, 8, cartilage from the extremity of the tibia in a young rabbit: 7, corpuscles which have rapidly divided from the middle of one of the longitudinal series; 8, nucleated corpuscle from near the ossifying surface of the same series. All × 600.

lopment with the rest of the skeleton, constituting the permanent cartilages of the nose, joints, *symphyses*, and *synchondroses* ;

by any one who will without prejudice examine into the subject, but it seems to result from the observations, even of those who have interpreted the facts otherwise.

Schwann ('Mikros. Unters.,' pp. 112, 113) describing the development of the cartilage of *Pelobates*, says: "The new cells arise in the cytoblastema (matrix *nobis*). . . . . . We see at first mere cell-nuclei (corpuscles *nobis*), which are somewhat smaller than the nuclei of the full-grown cells, *a*, *b*; partly nuclei, which are closely surrounded by a cell, *c*, *c*; in short, all transitional forms, from mere cell-nuclei and nuclei surrounded by small cells, to fully formed cells; so that here, development takes place as in small cells, and the nucleus is their actual cytoblast. . . . . . The cell-membrane becomes distinct only in the full-grown state."

In the next page, Schwann speaks of the free-swimming nucleated corpuscles which he obtained from the ossifying cartilage of a fœtal pig, and which he considers to be identical with the bodies already described in *Pelobates*. In reality, however, these bodies are not cells in the same sense, being merely the nuclei of Schwann and the nucleated form of the corpuscles to which we have referred above.

Whatever Schwann's words may indicate, then, his observations tend to precisely the same conclusion as our own.

Henle ('Allg. Anat.,' pp. 803—808) follows Schwann, and equally fails to discriminate the cells in *Pelobates* from the "cells" in the fœtal pig.

Reichert (in his admirable work, 'Ueber das Bindegewebe,' 1845) recognises the fact that the cartilage-corpuscles are "nuclei" in Schwann's sense, and refers the appearance of a distinct wall in the cavities, to an optical delusion. He asserts that young cartilage is composed of distinct cells closely united together, without any measurable intercellular substance; as the cartilage grows, the latter increases, and eventually the cell-walls disappear. The only evidence of the existence of these cells and intercellular substance offered by Reichert, however, is the mode in which the tissue may be broken up; a kind of evidence whose value the purport of the rest of his book is to reduce (and most successfully) to nothing.

In effect, therefore, Reichert's observations come to the result already stated, that the fœtal cartilage is composed of a homogeneous matrix, in which the corpuscles are dispersed.

Robin ('Observations sur l'Osteogenie') takes nearly the same view of the structure of cartilage as that we have indicated. "Cartilage is composed," he says, "of a homogeneous, amorphous, dense, elastic, hyaline basis (*substance fondamentale*), in which cavities are hollowed out,—the *cartilage-cavities*. In each of these cavities we find one or many (sometimes 20 to 30) cells,—*cartilage-cells*, whose parietes cannot be demonstrated to be distinct from their cavity. These cells are more or less granular, and have a nucleolated nucleus. . . . . . In the fœtus, up to the age of four or five months, more or less, the cartilage cavities do not inclose one or more cells, but one or many masses of yellowish granulations, all of nearly the same size. These masses are more or less distinctly defined at their edges, in general indistinctly, and nearly reproduce the form of the cavity without ever filling it. They may be called *cartilage-corpuscles*. Authors have not generally remarked this fact. By degrees the cells which replace these corpuscles are developed. These cells are formed all at once;

a second disappears altogether in the course of development (certain cranial cartilages, *vide* § 101); the third and greatest

but the grades of the process as regards the commencing cell or the pre-existing granulations are as yet but little known. . . . . . Some authors wrongly call the cavities excavated in the fundamental substance, *cartilage-cells;* and to the true cartilage-cells and masses of yellowish granulations or corpuscles referred to above as existing in the fœtal state alone, they give the name of *contents*."

Remak ('Ueber die Entstehung des Bindegewebes und des Knorpels,' Müller's 'Archiv,' 1851-2) appears to have been the first, definitely to recognise the cartilage-corpuscles, as the homologues of the primordial utricles of plants,—a great step, and one which appears to us to lead to most important consequences. Like Schwann, however, led away by the generally assumed anatomical independence of the vegetable cells, Remak interprets the structure of cartilage in the same manner, and speaks of the secretion of the chondrinous wall by the primordial utricles, as "parietal-substance" within the primary cell-membranes. He adduces no evidence, however, that the *facts* are other than as we have stated them to be.

Virchow ('Die Identitat von Knochen-, Knorpel-, und Bindegewebe-körperchen so wie über Schleimgewebe, 'Verhandlung d. Phys. Med. Gesellschaft,' 1852) is an important witness in this matter. He says, "I have anew convinced myself that the so-called cartilage-corpuscles are actual cells which lie in a cavity of the basis (*Grundsubstanz*) or in a cell-cavity presenting a double contour, and possess a membrane, granular contents, and a frequently nucleolated nucleus. In the neighbourhood of the line of ossification, in growing cartilages, as well as in the young callus-cartilage of fractures, these cells are of very large size, clear, and round; in the neighbourhood of the articular extremities, excessively small, compressed, and dark. Under favorable circumstances, the cells, in simple cartilage, may be isolated, and their peculiar relations with regard to acetic acid, which generally renders them darker and collapsed, may be exhibited. Water also causes them to collapse, and they thus occasionally form peculiar, jagged corpuscles, which one might be readily tempted to confound with branched cells. The larger the original cell was, so much the more branched does its collapsed mass appear. . . . . ." (p. 152.) "It might have been expected that in the course of ossification of the cartilage, these cells would be seen to pass into the irregular, anastomosing bone-corpuscles; but nothing of the kind is visible. . . . . . A point of difficult determination is, in general, the existence of actual cells in the small flat cavities of cartilage, *e. g.* towards the surface. Very frequently it would here seem as if the membrane of the cell had coalesced with the intercellular substance, and only the contents with the nucleus had remained behind. But on careful investigation, especially under the prolonged operation of acetic acid, frequently after maceration in hydrochloric acid, we clearly see a complete cell with a nucleus and contents in the cavity" (p. 153).

Virchow gives no figures, but the above passages furnish so accurate an account of what we have ourselves seen in young and in fully-formed cartilage, that we have thought we could not do better than cite them. The jagged appearance of the corpuscles to which he refers, is very common, and we have been led to suspect that it may arise from the same cause as the very similar appearance often exhibited by the colourless corpuscles of the blood, viz. a protean throwing out of processes. In fig. 129 *A*, we have represented cartilage corpuscles of the forms which he describes;

part, ultimately becomes ossified, and constitutes all the bones of the trunk and extremities, and a great part of those of the cranium. All these bones are ossified, essentially, in the same way. At one or more points (*puncta ossificationis*), in their interior, a deposition of calcareous matter commences, simultaneously with a change in the cartilaginous elements; which transformation proceeds on some, or on all sides, continually converting additional portions of the cartilage into bone. Whilst this is going on, the cartilage, in most cases, ceases to

5, 8, are nucleated corpuscles from the Kitten and Rabbit; 6, "jagged" corpuscles from the Kitten.

When Virchow, however, describes the passage of these "cells" into the branched or stellate corpuscles of fibro-cartilage, and considers the latter to be metamorphosed cartilage-corpuscles, he confounds together things which are essentially different. Careful examination of fœtal fibro-cartilage, *e. g.* the intervertebral fibro-cartilage of the Kitten, shows that the stellate body is the *wall of the cartilage cavity*, with processes which run out from it, the original corpuscle remaining in the interior of the cavity, either unchanged or becoming gradually lost, or fused into one mass with its walls.

The account of the structure of cartilage given by Tomes and De Morgan (l. c., pp. 15, 16) in all essential points agrees with that of Virchow. They call the corpuscles, *granular cartilage cells*.

To recapitulate:—the *facts* contained in other observations, as apart from the *interpretation*, appear to agree perfectly with our own; the result of which is, that in the fœtal state, cartilage is composed of a homogeneous matrix, in which lie the corpuscles, in cavities which they just fill; that their relation to the matrix is exactly that of the primordial utricles to the cellulose wall in plants, and that like this they may or may not develope a nucleus; that with age they enlarge, but not so fast as the cavities, the walls of which become chemically altered into chondrin, a change which often takes place in such a manner as to give rise to a lamination or to a difference in composition of the inner and outer portions. If the cartilage be converted into fibro-cartilage, the outer part becomes changed into collagen, while an alteration into a substance resembling elastic fibre, is effected in the inner portion, and in the direction of certain lines radiating from it, just as we have seen the elastic element to be developed in connective tissue (see § on Connective Tissue).

So much for the structure of cartilage: with regard to its development and multiplication we must equally demur to the statements in the text. It is, indeed, very true, that no new cartilage-cells arise independently of those which pre-exist; but in opposition to Professor Kölliker we must agree with Leydig, Robin, Remak, and Tomes and De Morgan, that the multiplication of the cartilage-cells invariably takes place by a process of division exactly analogous to that which occurs in plants. So far as we have seen (and in ossifying cartilages, and in that of the Skate, it is easy to trace the process), the corpuscles first become constricted (fig. 129 *A*, 3), being found occasionally of an hour-glass shape; and eventually divide (2, 3, 4, 7). The matrix then grows in, so as to separate the two, and the process of fission is complete.—Eds.]

grow in one direction, and, consequently, is there soon entirely converted into bone, whilst in others its growth continues, so that a new cartilaginous, plastic material is furnished for the progressive increase of the bone, which material, as in the epiphyses of the cylindrical bones, is sometimes developed into distinct ossific centres or nuclei. When the whole of the cartilage has been converted, and its *perichondrium* become *periosteum*, the bone does not cease to enlarge, but a new and peculiar mode of formation is now set up, in all these places, until its growth is completed. This consists in the ossification, from that surface which is in contact with the bone, of an organised, soft, plastic material, which is deposited on the inner surface of the highly vascular *periosteum*, and in proportion as this conversion into bone takes place on the one side, fresh, fluid materials for it are afforded by the *periosteum* on the other.

§ 103.

Changes in the ossifying Cartilage.—The active vegetative process in the cartilage-cells when ossification is going on, depends upon this,—that the cells which were hitherto of small size, and contained but few secondary cells, begin to grow, and successive generations of cells to be produced in them, as may, also, be seen at the ossifying margins of bones already existing, in which situation larger cells may be noticed close to the bone, and others, which are smaller in proportion to their distance from it. All the cells which are engaged in the incipient formation of the bone, present clearer and, less frequently, granular contents, a distinct, vesicular, round nucleus, with nucleolus and readily distinguishable walls; they are very quickly altered, however, on the addition of water, acetic acid, alcohol, and by drying, &c., so that the contents contract around the nucleus, and form a roundish, elongated, irregular, even stellate, granular, opaque body (*cartilage-corpuscle* Autor). Their size and mode of grouping vary, not inconsiderably, according to age and situation. With respect to the former, they exhibit during embryonic life a constant increase, whilst after birth they appear to retain a uniform size; and, as regards the latter, it may be stated as a law, that where the ossification of the cartilage proceeds in one direction only, the cells, at the osseous border, are disposed

in *rows*. This is most distinctly seen, as has been long well known, in the extremities of the *diaphyses* of the larger cylindrical bones, where the rows of cells are very prettily arranged in parallel lines close together, and are of considerable length; it is also evident in the other long bones, as well as in many others where the cartilage ossifies only on one side, as in the connecting surfaces of the *vertebræ*. Where, however, the ossific nuclei in the centre of a cartilage enlarge on all sides, the cartilage-cells are confusedly grouped in roundish, or oval, irregular little masses, as in the short bones at their first formation, and in the *epiphyses*. An accurate comparison of the cells which are closer to the ossifying margin, with those more remote from it, and of the groups formed by them, at once shows that their particular disposition is directly related to their mode of increase, Each individual group (or even two of them) corresponds, in a certain measure, with a *single* primordial cell, and represents all the descendants which in course of development have proceeded from it. In the one case, all these newly-formed cells are disposed, one behind the other, in a single or double, linear series; and in this way are produced, by their further increase, the rows of cells above described, whilst in the other they con-

Fig. 130.

Fig. 130. Perpendicular section from the ossifying border of the shaft of the femur of a child a fortnight old, × 20 diam.: *a*, cartilage, in which the cells the nearer they are to the ossifying border are placed together in more extended longitudinal rows; *b*, ossifying border, the dark streaks indicate the progressive ossification in the intercellular substance, the clearer lines the cartilage cells which ossify subsequently; *c*, compact layer of bone near the ossifying border; *d*, the *substantia spongiosa* formed in the osseous substance by resorption, with cancelli, the contents of which are not shown.

stitute a more globular mass. The primordial cells (first parent-cells) during this procedure, sometimes disappear as distinct organisms, owing to the coalescence or fusion of their walls with the interstitial substance, sometimes not; and the same holds good with those of the subsequent generations. The latter is usually the case in the rounded masses of cells, owing to their smaller size, and around them a contour line may for the most part be recognised, which is nothing more than the distended wall of the first cell; whilst in the *rows* of cells, the walls of the original cells are not, usually, so merged in the intercellular substance as to escape recognition. The entire matrix, in which the just-described, enlarged, and actively multiplying cells are enclosed, varies very considerably in thickness in the different cartilages; scanty around the osseous nuclei in the *epiphyses* and short bones, it is $\frac{1}{4}$ to $\frac{1}{2}'''$ thick in the *diaphyses*. It is universally characterised by its yellowish, transparent colour, and its streaky, apparently fibrous fundamental structure, from the other cartilaginous parts, which are, as usual, blueish-white, with a homogeneous or granular interstitial substance.

Fig. 131.

The *vessels* met with in the ossifying cartilages constitute a phenomenon well worth attention; from the middle of fœtal life onwards, they occur in many situations, preceding by a shorter or longer time the appearance of the osseous nuclei, and accompanying their increase. I have observed them in the articular cartilage of the epiphyses of the long bones even in a person 18 years old. They entered the cartilage

Fig. 131. *Femur* of a child a fortnight old, natural size: *a*, *substantia compacta* of the shaft; *b*, medullary cavity; *c*, *substantia spongiosa* of the shaft; *d*, cartilaginous *epiphyses* with vascular canals; *e*, osseous nucleus in the inferior *epiphysis*.

in great number, perpendicularly from the bone, ramifying, and terminating a little below its free surface. The cartilage-vessels invariably lie in wide canals (measuring, even in a five-months' fœtus, 0·02—0·04‴) excavated in the cartilage, and bounded by narrow, elongated cartilage-cells,—the *vascular canals of cartilage*, or *cartilage canals*,—which enter the cartilage from the perichondrium, and, when a vascular ossific nucleus exists (*diaphysis*), also from the border of the ossifying portion itself (though in less number, at all events at an earlier period), penetrate it in straight lines, in various directions, giving off a few branches, and, to all appearance without any anastomoses, or other kind of interconnection, end, for the most part, in blind, club-shaped dilatations. These canals are produced by a resolution of the elements of the cartilage, in the same way as the medullary cavities of the bone itself, originally contain a plastic material composed of minute rounded cells (cartilage-marrow), corresponding to the fœtal cartilage-marrow, and develope in a short time out of this material, true sanguiferous vessels, and a wall composed of more or less developed connective tissue, and subsequently also of elastic fibrils. As concerns the vessels themselves, I have sometimes found, in a canal, only one large vessel (frequently very distinctly arterial, with muscular walls), sometimes two such, sometimes capillaries in various numbers, but I am unable to explain how the circulation is carried on in these vessels. There must either be anastomoses between the vessels of different canals, or if the latter be really closed, arteries and veins both probably exist in one and the same canal. The object of these vessels of cartilage appears to be of a double character; in the first place, to convey the materials requisite for its growth and further development; and secondly, to promote the ossification. The former of these functions is very manifestly carried out in the thick epiphysal cartilages, which grow to such a length before they become ossified, and even afterwards continue to enlarge; and the latter is probably effected principally in the short bones, which do not contain vessels until just before the commencement of ossification. Notwithstanding this, however, it is not intended to imply, that a cartilage cannot grow, nor become ossified *without* vessels; but although the latter condition does in fact obtain in animals, and probably also in man,

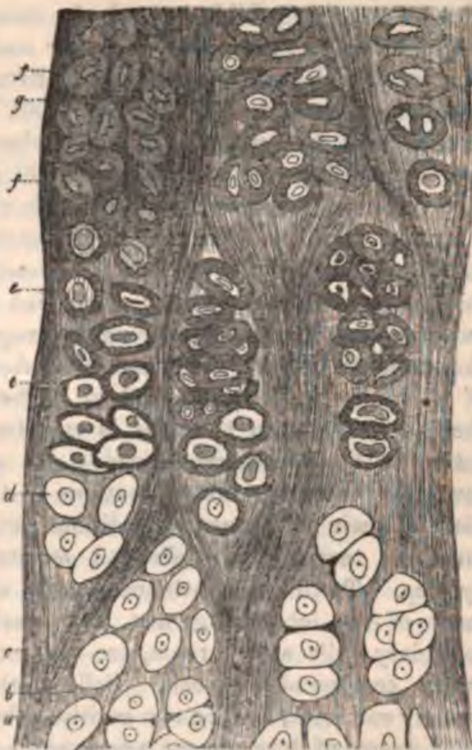
normally in certain situations (on the appearance of the first points of ossification of the embryo, those of the *ossicula auditus*, &c.), still, this does not prove that the vessels when existing have no concern in the processes adverted to; and consequently it cannot be admitted, as lately supposed by H. Meyer, that they are to be regarded in the light of accidental productions, and as standing in no necessary relation with the development of the bone.

§ 104.

Ossification of the Cartilage.—The ossification of the matrix generally precedes in some degree that of the cartilage-cells; and, under normal conditions, is primarily effected by a granular deposition of calcareous salts (calcareous granules as they are termed). Where the cells are disposed in rows, at the ossifying border, this deposition of earthy matter always proceeds in the fibrous substance between the rows of cells, forming processes, which, in a longitudinal section, assume the appearance of pointed teeth, and surround the lowest portions of the rows of cells like short tubes. The same disposition, essentially, is also manifested in other situations, where the cartilage-cells constitute more rounded groups, only, that in this case the ossifying matrix surrounds them more in a reticular manner. The *calcareous granules or particles*, the first visible deposit of the earthy salts of bones, are of a rounded angular figure, white by reflected, opaque by transmitted light, easily dissolved with effervescence in acids, and differing in size in different bones, from immeasurable minuteness up to 0·001‴, or even 0·002‴; their size, however, does not appear to be regulated by period or situation, although there is no doubt that they are frequently, in one place, of uniform minuteness, and in others uniformly of coarser character, but rather by some change occurring in the supply of plastic material to the ossifying border. If this earthy deposit be traced in microscopical sections, from the margin of the ossification into the interior of the young bone, it will be apparent, that it is to it, for a certain distance, although with diminishing distinctness, that the granular and opaque aspect of the margin itself is due; the substance gradually becomes more homogeneous, clearer and more transparent, ultimately acquiring the aspect

of perfect bone. According to all appearance, the primordial earthy granules or particles become gradually fused together, and thus impregnate the whole tissue of the matrix of the cartilage, instead of, as before, separate portions, and thenceforth disappear as isolated, distinguishable particles.

Fig. 132.



With respect to the *formation of the bone-cells*, I believe, that owing to the discovery of an excellent subject for their observation, viz. rachitic bone, I have put the matter, as regards the most essential particulars, in a clear point of view. The bone-cells are formed,—as Schwann thought possible, and Henle supposed, from analogy with the lignified vegetable cell with pores or dotted canals,—from the cartilage-cells, by the thickening of their wall, with the simultaneous formation of canalicular vacuities in it, and its ossification. In the ossifying shaft of a rickety bone (fig. 132) the morphology of this process may be most beautifully observed. If the rows of cartilage-cells of the ossifying

Fig. 132. From the ossifying border of the condyle of the *femur* of a rachitic child, two years old, × 300 diam.: *a*, cartilage cells, simple and parent cells in series; *b*, more homogeneous; *c*, striated matrix between them; *d*, cartilage-cells at the commencement of their transformation into bone-cells; *e*, the same further advanced, with very much thickened walls, indication of canaliculi, commencing deposition of calcareous matter in the walls, whence their darker colour, though still with distinct nuclei; *f*, bone-cells still more developed and more ossified, in an equally ossified matrix.

border, which in this case are of larger size, be traced from without to within, it will soon be found, that at the point where the deposition of calcareous salts (which takes place for the most part without the formation of the calcareous granules) commences, they exhibit, instead of a membrane indicated by a single, tolerably strong line, a thicker coat, which on the inner side presents delicate indentations. Even when the thickness of this membrane does not exceed 0·001‴ (fig. 132, *d*), it is obvious that the cartilage-cells are about to be transformed into bone-cells; and this becomes still more evident, when, further on in the bone, the thickness of the membranes in question, together with the simultaneous diminution of the cavity of the cell, is seen to be constantly increasing, the indentations of the interior contour line to become more and more marked, and, accompanying the progress of these changes, the walls to become more and more dark from the addition of calcareous matter (fig. 132, *e*). The slow ossification of the matrix between the cells is very favorable to the observation of these changes, allowing not only of the accurate investigation of the first alterations in the cartilage-cells, but also of their subsequent conditions, at a time when they must be termed *bone-cells* and *lacunæ*, being traced step by step. To this circumstance alone is also due the establishment of the interesting fact, that cartilage-cells, enclosing secondary cells within them, are converted, as a *whole*, into a single, compound bone-cell. Cells of this kind are very frequently met with, having two cavities, which cells, according to their degree of development, are sometimes wide and furnished with short prolongations, and sometimes, from their contracted cavity and long canaliculi, resemble in all respects perfect bone-lacunæ. Compound cells, with 3, 4, and 5 cavities, each with the remains of the original contents and nucleus, occur more rarely, though even such are occasionally to be found in almost every preparation. The cartilage-cells lying free, and in close apposition, though in a non-ossified matrix, having thus evidently become transformed into bone-cells with nuclei and other contents, the ultimate changes now take place from which the rickety bone-substance acquires pretty nearly the nature of the sound tissue. These changes, in as far as they affect the bone-cells, chiefly depend, in the first place, upon the com-

mencement of ossification in the matrix, but without any primary formation of calcareous particles; and secondly, upon the continually increasing deposition of earthy matter in it, and in the thickened cell-walls, owing to which, the new bone-substance, to the naked eye becomes more and more white, and under the microscope appears more and more dark and transparent; it now, also, becomes more homogeneous, and the abrupt limits of the bone-cells gradually less and less defined, till at last they appear, not as cellular organisms lodged in the matrix, but to be confused with it, being recognisable only from their peculiar stellate cavities,—the so-termed *bone-corpuscles*, or *lacunæ and canaliculi*.

With the knowledge thus obtained of the formation of the *lacunæ* in rachitic bone, the endeavour to arrive at an insight into the same process in normal bone, is no longer attended with as much difficulty as before, when the inquirer was involved in a maze of hypotheses of the most various kinds, and all without any certain foundation. The investigation of the conditions attending the development of bone, both in man and other animals, must nevertheless still be regarded as troublesome, and frequently little worth the pains bestowed upon it. It is, perhaps, certainly manifest (*vid.* 'Mik. Anat.,' tab. iii, fig. 6), that the bone-cells, a little beyond the limit of ossification, become thickened, and, still presenting the remains of their cavity and the nucleus, beset with calcareous particles; and although such encrusted cells may even be isolated, yet the mode in which the changes are effected further on, is not, beyond a short distance, I must affirm, to be seen with anything like the distinctness that it is in rachitic bone, because, more internally, the newly-formed medulla with its vessels, and the calcareous particles, render almost everything indistinct; and it is not till we get to the homogeneous and more transparent osseous tissue beyond, that distinct, but almost perfectly-formed lacunæ come into view. Nevertheless, from all that we see, there cannot be the least doubt, but that the processes are essentially the same as in *rachitis*, only, that in the healthy bone the ossification of the thickened walls of the cartilage-cells, presents two stages, instead of only one, as in the former case, inasmuch as they first appear granular from the deposition of the calcareous particles, and afterwards homogeneous. More-

over, even in perfectly normal bone, in the adult, I have met with places (some of which, independently of me, have also been lately described by H. Meyer (l. c.)), such as the *symphysis pubis*, the *synchondroses* of the *vertebræ*, and those of the *ilium*, *sacrum*, and the points of insertion into the bones of certain tendons containing cartilage-cells. In all of these situations, at the line of junction between the cartilage or tendon and the bone, cartilage-cells of the most characteristic aspect may be seen, lying free in the cartilaginous matrix, and presenting the most various degrees of transformation into bone-cells; some, in particular, having thickened walls, and a more or less copious deposit of calcareous particles; while others are almost perfectly-formed bone-cells, with pores and a more homogeneous wall (fig. 123); so that I am able to afford a certain support to the statement given above with respect to the mode of origin of the bone-cells, by the conditions presented in normal tissues also. In the last-named situations I have, likewise, very distinctly and very frequently noticed, half or wholly ossified parent-cells, containing from 2 to 12 secondary cells.

There is another point in the development of the bone-cells still obscure, or at least that has not been directly observed, viz.: how their pores or canaliculi become branched cavities, communicate with those of other cells, and acquire open orifices in certain situations. All that is apparent in rachitic bone and elsewhere, is merely the circumstance, that the thickening of the ossifying cartilage-cells does not proceed with a straight but with an indented border, which is the case in fact from the beginning up to their completion, and that the bone-cells have, at first, more simple prolongations than afterwards. Observation teaches nothing beyond this. Now, as there can be no doubt that the canaliculi anastomose very freely, and also, that they frequently open on the outer surface of the bone, or into the cavities in its interior, I do not for a moment hesitate to express the opinion, *that the canaliculi, arising as simple branches from the lacunæ, are continued or further developed by absorption of the already formed bone-substance.* How such an absorption takes place, cannot, it must be confessed, be explained; but that affords no ground of objection to the opinion, because we see a similar process,

though on a widely different scale, take place in the formation of the medullary cavities and cancelli (*vid. infra*). It would appear to me, that currents of the nutritive fluid in the bone were chiefly concerned in this further development of the *canaliculi;* and the more so, because the first rudiments of the *canaliculi*, like the pore-canals of lignifying plant-cells, manifestly indicate nothing more than the points at which the ossifying cartilage-cells continue to admit and emit fluid; on which account, also, their direction is principally towards the internal and external surfaces of the bone, from which the nutritive plasma is derived. It appears to me highly probable, that after the complete ossification of the cartilaginous tissue, the nutritive fluid derived from the blood-vessels of the periosteum and of the medullary cavities (1.) finds new ways for itself towards the *lacunæ* and their prolongations, which, as it may be said, alone are still open to it, and in this way effects their opening on the internal and external surfaces of the bone, and (2.), also burrows passages from the cavities lying nearest to it, and thus ultimately produces a ramification of them, and brings about numerous communications between the different cavities. In accordance with which, a secondary formation of *canaliculi* must take place, not only in the region of the thickened walls of the original cells, but also in the osseous matrix, and this to a considerable extent, as is at once evident, when the distances between the anastomosing cavities are compared with the diameter of the original cartilage-cells.

The *development of the medullary* spaces (*cancelli*) and of the medulla, is to a certain extent the last act in the transformation of cartilage into bone. The medullary spaces do not arise in a coalescence of the cartilage-cells, but from a solution of the more or less perfectly formed bone-substance, exactly like the large medullary cavities of the cylindrical bones. This is most distinctly and satisfactorily shown by the examination of the diaphyses of a sound or rachitic bone, but especially in the latter. At the limit of the ossification itself, the osseous tissue for a distance of about $\frac{1}{5}$ to $\frac{1}{3}'''$ is quite compact, without a trace of larger cavities, and is composed in part of the ossified matrix, and in part of cartilage-cells, more or less advanced in their transformation into bone-cells ('Mik. Anat.,' tab. iii); beyond this part, however, cavities, at

first small, and more internally, larger, come into view, the whole relations of which show most convincingly that they do not originate in any development of the existing elements. They have an extremely irregular contour, are oval, or roundish and angular, and for the most part broader than the cartilage-cells, appearing to be eaten out, as it were, in the substance of the bone, and involving severally the compact tissue, matrix, and bone-cells. When the borders and limitary surfaces of these spaces are closely regarded, it is, in many instances, easy to notice bone-cells more or less removed, half projecting from, or buried in the wall, and between them projections of the ossified matrix, so that no doubt can any longer be entertained with respect to the origin of the cavities. It must be confessed that there is as little to be stated, in this case, as in that of the origin of the analogous cartilage-canals, and the further development of the *canaliculi* of the bone-cells, with respect to the mode in which this absorption takes place; and the process is even still more inexplicable, because, allowing that it really does take place, there would then exist in the ossifying bone, at the same time and almost in immediate contiguity, a formation of bone and a resolution of the tissue, but very little less energetic. The above-described mode of formation of the *cancelli*, nevertheless, is a morphological fact, and consequently, the explanation of such a curious phenomenon becomes a problem to be solved by chemistry and physiology. As in the *diaphyses*, so in the ossification of all the other cartilages, medullary spaces are formed by the resorption of the inner portions of that part which is half ossified. But it must be stated, that these spaces do not present the same form, direction, and size in every bone; though with respect to this, it is unnecessary to offer any special remarks, since the relations of this primitive spongy substance are, in the main, the same as they are afterwards. Still, it may be remarked, that in many bones, solitary spaces are apparently developed immediately from cartilage-canals, seeing that some at least of the latter, at the limit of ossification, communicate directly with the spaces in the bone; and, moreover, that not unfrequently, cartilaginous elements not yet wholly converted into bone-cells, are drawn into the process of resolution.

The medullary cavities, however they arise, are filled with a

soft, reddish substance—*fœtal medulla*. This substance at first consists of nothing but a small quantity of fluid and many rounded cells, with one or two nuclei and faintly granular contents, of which I am unable to say how they originate, but only this much, that they are altogether new formations. In process of time these cells, which are in all respects identical with those which occur, in the adult, in certain bones (*vid. supra*), are developed in the usual way into connective tissue, blood-vessels, fat-cells, and nerves. The formation of blood-vessels proceeds with great rapidity, so that the bones, very shortly after the development of the medullary spaces, exhibit blood-vessels in them; that of the fat and nerves takes place more slowly, although the latter, at the period of birth, of course with fewer filaments than subsequently, may be very readily perceived in the large cylindrical bones, even more readily than in the adult, because at this time the medulla may be more easily washed away from them and the great vessels. The fat-cells at this period are but few in number; the medulla, in man at least, being coloured entirely red by the blood and the light reddish medulla-cells. After birth they gradually multiply, till at last, the marrow, in consequence of their great increase and the disappearance of the medulla-cells, which are ultimately all transformed into the elementary tissues of the permanent medulla, acquires its subsequent colour and consistence.

In many of the primarily cartilaginous bones of Birds and Amphibia, the ossification of the cartilage commences, according to Rathke and Reichert (l. c.), on the outer aspect of the cartilage, so that at first a cylinder of bone is formed with cartilage internally and at the extremities. The remainder of the internal cartilage then affords space to the medulla, whilst the epiphyses are formed out of that of the extremities.

[If the contents of the cartilage-cells, the "cartilage-corpuscles" of authors, be really surrounded by a membrane, as Virchow supposes, it may be assumed that a similar tunic, analogous to the primordial utricle of the plant-cell (*vid. sup.* § 8), exists also around the contents of the bone-cells, and that it takes an essential part, by its throwing out stellate processes, in the first formation of the *canaliculi*, their further elonga-

tion and ultimate anastomoses. In this case, also, the stellate and readily isolated cartilage-cells from an *enchondroma* described by Virchow (Würz. 'Verh.,' Bd. 1), around the internal portions of which the contours of rounded cells were visible would be intelligible, and even the possibility of the isolation of stellate organisms from normal bone (*vid. sup.*) be explicable. My exposition of the formation of the *lacunæ* in rachitic bone, is confirmed by Rokitansky and Virchow (Würz. 'Verh.,' II); whilst Robin declares that it is incorrect, giving a description of their formation which is, to me, unintelligible. I recommend to his notice rachitic bone, the *cementum* of the horse's tooth, and the *symphyses* (§ 95), with which he is manifestly unacquainted, and hope that he may then be induced no longer to regard Schwann's and my views as antiquated.[1]]

[1] [As we have already said, we must deny the existence of endogenous cell-development in ossifying, or any other cartilage. In fact, the process of multiplication of the corpuscles (nuclei (?) of Kölliker, granular cartilage-cells of Tomes and De Morgan) is so clear, that we are at a loss to comprehend how it can be mistaken. What is meant in the text by "contents," as distinct from the corpuscles, we do not know. Messrs. Tomes and De Morgan describe the real changes which precede ossification, very exactly in a few words, thus: "Cartilage previous to its conversion into bone undergoes a rapid growth, which takes place principally in the direction of the long axis of the future bone. Each granular cell becomes divided into two, by segmentation transverse to the line of ossific advance. These are again divided, and the process repeated from time to time, until in the place of a single granular cell we have a long line of cells extending from the unchanged cartilage to the point where ossification has taken place" (l. c., p. 16). "If attention be directed to the end of the line furthest from the bone, the cells will be found small in size, granular, and with a perceptible nucleus, but without an outer wall, distinguishable from the hyaline substance, which is abundant between the contiguous lines, but small in quantity between the cells composing the lines. But if the other end of the line be examined, very different conditions will be observed. The granular cells will be seen to have become rounded in form, to have increased to three times their original bulk, and to possess well-marked, circular nuclei. . . . . ." p. 17. (See fig. 129 *A*, 8.)

So far, our own observations are in perfect accordance with those of Tomes and De Morgan. They go on, however, to observe, "in addition to which, each granular cell will have acquired a thick, pellucid, outer wall;" and with this last statement we can by no means agree. Neither in Man, the Calf, the Rabbit, the Skate, nor in enchondroma, have we been able to see anything of the regular development of such an envelope: in fact, in the great majority of instances, we have convinced ourselves of the absence of anything of the kind—there being nothing but a clear space between the corpuscle and the ossified wall of the cavity in which it lies. Bodies corresponding with the lacunal cells—cartilage-corpuscles that is,—invested

§ 105.

Elementary processes in the Layers formed from the Periosteum.—The periosteum of the primarily cartilaginous bones, is proportionally very thick and vascular, consisting, as early as at the fifth month, of common connective tissue and fine elastic filaments, the latter of which in process of time become stronger and stronger, occasionally assuming the nature of elastic fibres. On the inner aspect of this fully formed periosteum, there is now deposited an *ossific blastema* firmly adherent to the bone

by a thick coat of more or less granular, calcareous matter, may indeed often be obtained free; but they arise, like the corresponding bodies in rickety bone, simply from the deposition of calcareous matter in the cartilage-cavity before it has taken place in the matrix, or from a want of union between the two deposits; and are therefore quite accidental.

The *lacunæ* are developed, according to these authors, by the shooting out of the granular cells into processes, and their direct conversion into the *lacunæ*, the nucleus of the granule-cell remaining as the nucleus of the *lacuna*. On this point also, we must differ from them, and agree with Virchow (l. c., note, § 101) and Kölliker (*supra*, § 104), that the development of the canaliculi is, by a process of resolution, quite independent of the corpuscles, which simply diminish in size, and either remain as the so-called "nuclei" of the lacunæ or totally disappear. We can especially recommend the Skate (fig. 136 *A*, 2) as a subject in which to trace the process of formation of lacunæ, as the bone is homogeneous and transparent, and in consequence of being inclosed in a large mass of firm cartilage, may be cut with ease into very thin sections. We have observed it with great clearness also in enchondroma.

There is one argument which seems to us conclusive on this point. Wherever the canaliculi can be seen at all, however young the tissue, they are perfectly clear and transparent. If, however, they were formed by processes of the granular cells, they ought to be granular, and more or less opaque.

Taking the same view of the structure of cartilage as Messrs. Tomes and De Morgan, then, our view of the nature of the lacunæ, resulting from its ossification, agrees with that of Professor Kölliker. Cartilage becomes bone by the deposit of calcareous salts in the matrix, and occasionally in its cavities. The lacunæ are spaces left round the corpuscles, from which, by resorption, processes—the canaliculi,—are subsequently developed. If it be asked how it is that the lacunæ may frequently be demonstrated both optically and chemically as distinct bodies, we must call to mind the fact already referred to, that in cartilage, the walls of the cavities have frequently undergone less change than, or a different change from, the surrounding matrix; and therefore appear both optically and chemically distinct, though they are by no means so, morphologically: and, therefore, that there is no difficulty in supposing the same thing to occur in bone. The chemical differentiation of the wall of the lacuna is, in fact, exactly comparable to that of the wall of the cavity which contains the "nucleus" in connective tissue, and in fibro-cartilage; and which gives rise to the formation of the elastic element in those tissues.—Eds.]

(fig.133,B); so that when the periosteum is removed, it generally remains upon it as a moderately thick, soft, whitish yellow lamella, in which, microscopic examination shows the existence of a fibrous tissue, with a not particularly distinct fibrillar formation, something like immature connective tissue, and granular, oval, or round nucleated cells, measuring 0·006—0·01‴. When this lamella is raised from the bone, it is found to be very intimately connected with the most superficial layers, and on its internal surface a few little detached fragments of bone, and scattered masses of reddish, soft medulla, from the most superficial cancellar spaces, will be observed. The bone thus laid bare, when the removal of the periosteal layer has been carefully conducted, presents a rough, and as it were porous surface, with numerous medullary spaces, and remains, superficially, in spots of greater or less extent, quite soft, pale-yellow, and transparent, whilst more internally it becomes firmer and whiter, ultimately acquiring the usual appearance of perfect osseous tissue. When it is inquired, how the formation of bone, which indubitably takes place in this situation, is effected, we refer to the blastema just described, the cells of which, scattered in the fibrillated connective tissue, have not the least resemblance to those of cartilage, but appear exactly like the fœtal medulla-cells, or formative cells of the embryo. In fact, it is now, not difficult to show, that the outermost, still soft bone-lamellæ pass into the blastema in question, with their separate spiculæ and projections, and that (1.) the matrix of the bone arises from its fibrous tissue, by the simple uniform deposition of calcareous salts, although usually, as it seems, without the previous appearance of calcareous granules; and (2.) that the bone-cells are formed out of

Fig. 133.

Fig. 133. Transverse section from the surface of the shaft of the metatarsus of the Calf, × 45 diam.: *A*, periosteum; *B*, ossifying blastema; *C*, young layer of bone, with wide cavities, *a*, in which are lodged remains of the ossifying blastema, and reticular spiculæ, *b*, which towards the blastema present a tolerably abrupt border; *D*, more developed layer of bone, with Haversian canals, *c*, which are surrounded by their lamellæ.

the formative cells of the blastema. With respect to the latter, however, the transformation cannot be followed step by step, as in rachitic bones. This much, however, is always apparent, that the bone-cells at first present larger cavities, less developed rays, and more distinct nuclei (the latter, as we know, remaining), and, as their occasionally visible outlines prove, correspond entirely in size with the cells just mentioned, so that I do not for a moment doubt, that they are formed in this situation exactly as they are elsewhere. With respect to the development of the ossifying blastema itself, it is at least clear, that it is derived from the numerous vessels of the fœtal and young periosteum; the origination of its fibres from fusiform cells, I have very frequently observed in man and in animals, but with respect to the cells, can only state that they occur of various sizes, and occasionally intermixed with free nuclei.

The formation of bone in this blastema occurs wherever it is in connexion with the bone; it does not, however, take place in *connected* but in *interrupted, reticular lamellæ.* The roundish or elongated spaces (fig. 133, *a*), which, from the first, remain between the layers of osseous tissue, and in the different layers communicate with each other, are nothing else than the *rudiments* of the *Haversian* or *vascular canals* of the compact substance, and contain a soft, reddish medulla, which at first is obviously nothing more than the unossified portion of the ossific blastema, although it sometimes contains more formative cells than connective tissue. The cells of these spaces are very soon transformed into the usual, light-reddish medulla-cells, and partly into vessels which communicate with those of the interior of the bone, and in part also with those of the periosteum, with which, having once formed a junction, they remain continuous during the entire growth of the bone in thickness, so that the formation of the spaces in the bone is, at least afterwards, preindicated by those, which, in accordance with what has been said, proceed from the periosteum through the ossific blastema to the bone. Besides medulla-cells and vessels as well as some connective tissue, the bone-cavities of the periosteal layers also contain round, elongated, or dentate, flattened, faintly granular cellular corpuscles of 0·01—0·02‴ or more in size, with from 3 to 12 or more vesicular nuclei and nucleoli, which are probably referable to the multiplication of the medulla-cells (*vid.* § 11).

The periosteal layers, which, agreeably to what has been stated, are from the first deposited in the form of cribriform lamellæ around the ossific-nuclei formed from cartilage, continue to be produced so long as the general growth of the bone goes on, essentially in the same way, constituting the material by which it increases in *thickness;* but at the same time, more or less important changes are set up in them; the most considerable of which take place in the *large cylindrical bones.* In these, we find, more distinctly indeed after birth, that a large cavity is gradually formed in the interior, which at first contains fœtal medulla-cells, and afterwards perfectly formed medulla. This medullary cavity is formed, in exact analogy with the medullary spaces described in the preceding paragraphs, by the solution of the osseous tissue of the shaft; at first, only of that which is formed from the primitive cartilaginous rudiment, but soon, also of that deposited from the periosteum upon the former, its development proceeding in a remarkable manner, as long as the general growth of the bone continues. Whence it comes to pass, that, as at the ends of the diaphyses, so also on its surfaces, *whilst new bone is continually deposited exteriorly, that which is already formed is as continually absorbed in the interior;* and in fact these two processes are so combined, that the bone, during its development is, in a certain measure, *several times* regenerated, and, for instance in the humerus of the adult, does not contain an atom of the osseous tissue which existed at the time of birth, nor does the bone at that period contain any of the tissue of which it was constituted in the embryo at three months. These conditions will be rendered most distinctly intelligible, and especially with respect to the periosteal and cartilage layers, by means of a diagram (fig. 134) which I have for a long time employed in my lectures. If, in this figure, we compare the primordial bone E E with the almost complete bone E^4 E^4, it is apparent, that in the longitudinal growth of the diaphysis of the latter on both sides, at the expense of the continually growing epiphysal cartilage, an elongated cone of osseous substance, 1, 2, 1^1 2^1, and 3, 4, 3^1, 4^1, is produced, to which, ultimately, the epiphysal nuclei E^4 E^4, also originating in the cartilage, are joined, whilst, to increase its thickness, the tubular layers P, P^1, P^2, P^3, which are constantly increasing in length and, in the middle, in thickness, are applied

to it. In a cylindrical bone of this kind consequently, the entire portion formed from cartilage, presents the figure of a double cone with rounded bases; and that formed from the periosteal layers, 1, 2, 3, 4, P^3, and 1^1, 2^1, 3^1, 4^1, P^3, the form of an elongated *tube* thickest in the middle, and resembling an elongated vertebra of a Fish, with conically hollowed, terminal surfaces. The articular cartilage C, is the unossified portion of the epiphysal cartilage, and the medullary cavity which is not shown in the figure (it may be supposed to be indicated pretty nearly by the outlines of the fourth bone E^3 E^3), is formed by the resorption of the entire osseous substance derived from the cartilage and periosteum of the younger bones;—in this case the first three, E E, E^1 E^1, and E^2 E^2.

Fig. 134.

In the cylindrical bones, without a medullary cavity, and in all other bones containing nothing but spongy substance in the interior, the absorption does not proceed to nearly the same extent as it does in the above-described cases, that is to say, only to the production of a looser spongy substance in the interior, and, consequently, we find, for instance in the vertebræ, more or

Fig. 134. Diagram of the growth of a cylindrical bone. *B*, primary rudiment, the diaphysis ossified and the epiphyses cartilaginous: *A*, the same bone in four stages of further advance, E^1PPE^1, $E^2P^1P^1E^2$, $E^3P^2P^2E^3$, $E^4P^3P^3E^4$; $P\,P^1P^2P^3$, periosteal layers of these four bones; the space contained within 1, 2, 3, 4, and 1^1, 2^1, 3^1, 4^1, indicates the portion which in the largest bones is formed from cartilage; E^1E^1, cartilaginous epiphyses of the second bone; E^2E^2, epiphyses of the third bone, in one of which is an osseous nucleus; E^3E^3, E^4E^4, epiphyses of the fourth and fifth bones, all with larger epiphysal nuclei: *G*, articular cartilage; *I*, *K*, interstitial cartilage between the ossified epiphysis and diaphysis.

less considerable remains even of the earlier bone-substance. In this situation also, the absorption always affects not merely the osseous nucleus, formed from the cartilage, but likewise the periosteal layers, the latest of which only remain more in their original form, as the *substantia compacta*.

The *Haversian canals* do not originate, as is sufficiently apparent from what has been said, like the cancelli of the primary bone-substance, from a solution of a pre-existing tissue, but are nothing more than *open cavities, left from the commencement, in the periosteal layers*. They are, relatively, of a considerable size at an early period, (*vid.* also 'Valentin. Entw.' p. 262), measuring in the fœtal humerus at five months 0·016—0·024‴, in the femur at birth, according to Harting (p. 78), 0·10—0·024‴, just as in the most recently formed layers also of a later period. Their contents have been already described. The most important circumstance connected with them remaining to be noticed, is the mode in which their lamellar systems originate. These lamellæ also are formed without the intervention of cartilage, and are nothing more than deposits from the contents of the canals, which substance, as has already been said, in respect of its fibres and cells, entirely corresponds with the ossific blastema beneath the periosteum, and, in a certain degree, is merely an originally unossified remainder of it. These conditions are easily observed in young bones, in which, the periosteal layers, before they have undergone any resolution, are rendered more and more compact by these new, secondary lamellæ; but even at a later period a more or less ossified blastema (always without calcareous granules) may very frequently be perceived on the walls of the canals in question. Whilst the vascular canals are thus, on the one side undergoing contraction by the deposition of these secondary layers, which, just as in the periosteum itself, appear laminated,—either because the ossific blastema itself is so constructed, or because the deposition of bone takes place with periodical pauses,—they afterwards widen, or at least some of them, by absorption, as for instance, the *canales nutritii*, the great vascular openings in the *apophyses*, &c.; and the compact substance, as has been already remarked, is also, in many places partially, and in some even entirely, absorbed.

In what way the bone increases in thickness in the situa-

tions where *tendons and ligaments, without the intervention of periosteum, are directly implanted into it*—has not yet been made out. From the circumstance, that in the *adult*, in many of these situations, true cartilage-cells occur among the tendinous fibres, and also, that their passage into bone-cells may very clearly be observed, it might perhaps be concluded that a similar process may take place at an earlier period also. In fact, I have seen, even in young individuals, at the points of insertion of many tendons and ligaments (*tendo Achillis, lig. calcaneo-cuboideum, aponeurosis plantaris, &c.*) into the bone, cartilage-cells, and their metamorphosis into bone-cells. Very frequently, also, tendons and ligaments are attached to portions of the bone which remain long in the cartilaginous condition, *epiphyses, tuberositas calcanei, &c.*, and the growth of these parts of course, is simply to be referred to the cartilage.

[The formation of bone on the inner aspect of the periosteum is a fact long well known, although it has, hitherto, generally been thought, that in this situation also, it was preceded by a thin cartilaginous layer, until the contrary was shown by Sharpey and myself. Since the discovery by Duhamel ('Mémoires de l'Academie de Paris,' 1742, p. 384, and 1743, p. 138), that the bones of animals fed upon madder are coloured red, a great number of experiments have been made with that substance, especially by Flourens, in growing animals; it being at first believed, that it only coloured those parts of the bones which were formed after its administration. This method, however, has lost a good deal of its value since it has been shown by Rutherford (in 'Roberti Blake, Hiberni, Dissert. inaugural. med. de dentium formatione et structurâ, in homine et in variis animalibus,' Edinb. 1780), Gibson ('Memoirs of the Literary and Philosophical Society of Manchester,' 2d series, vol. I, p. 146), Bibra (l. c.), Brullé and Huguény (l. c.), that when animals are fed upon madder, the whole of the growing bones, as well as the bones of adult animals, become coloured, and especially so wherever they are in more immediate connexion with the blood-vessels; for even the medulla is coloured (Bibra). For which reason also, the innermost layers of the Haversian canals, the periosteal surfaces, and the vascular, young bone-substance, acquire a deeper colour. There are, however,

still some points worth investigating in this way, particularly with relation to the more recent statements of Brullé and Huguény, who, relying upon the circumstance, that, as they assert, the decoloration of growing, coloured bones, is effected merely by the absorption of the coloured portions, believe they have found that the cylindrical bones also deposit osseous substance from within, particularly in the apophyses; whilst on the outer surface, absorption to the same extent takes place; statements upon which I will not, at present, give any decided opinion, although at the same time I hold it as quite certain, that in many places *an absorption does take place, on the exterior of the bone to a greater or less extent.* It is only by such an absorption that the enlargement of the *foramen magnum* from the sixth year upwards, at which time the portions of bone surrounding it are united, can be explained. And the same may be said with respect to the arches of the *vertebræ*, and numerous vascular and nerve-openings (*foramen ovale* and *rotundum* of the sphenoid bone, *foramina inter transversaria, canalis caroticus, &c. &c.*). Consequently, the law propounded by Serres (Meck. 'Archiv,' 1822, p. 455), that the openings in bone enlarge by the growth of the individual pieces by which they are bounded, is wholly incorrect, as applied to the openings and canals in the middle of bones; as had been already, to some extent, declared by E. H. Weber and Henle; and even in other cases it holds good only for the earliest periods.

The periosteal layers present a certain contrast to the osseous tissue developed from cartilage. The former constitute principally the firm cortex of the primarily cartilaginous bone, and are characterised by the occurrence of Haversian canals and their lamellar systems, whilst the latter produces the spongy substance, and contains no vascular canals. It must not, however, be forgotten that even the periosteal layers all have, at first, in a certain degree, a spongy structure, and in all these bones, without exception, contribute, and frequently very essentially, to the formation of the spongy substance; moreover, that in the cellular substance, which originates from the cartilage, in the *apophyses* for instance, secondary layers, similar to those of the Haversian canals, and of the spongy substance which is formed out of the periosteal layers, only not

so much developed, appear to be formed. The morphological and chemical relations of the matrix of these two forms of osseous tissue have not as yet been determined. On the other hand the bone-lacunæ of both kinds of tissue do not present the least difference.]

§ 106.

Bones not primarily cartilaginous occur, in Man, only in the cranium. They originate outside the primordial cranium, between it and the muscular system, and thus within the structures constituting the vertebral system. They by no means exist as membranous and cartilaginous capsules on the first appearance of the cranium, their formation not commencing till *after that of the primordial cranium, from a secondary blastema,* whence, in contradistinction to the other primary bones, the formative material of which exists prior to the commencement of ossification, they are termed *secondary bones*—or, also, because in most places they are in contact with portions of the primordial cranium—*covering or overlaying bones* (belegknochen). To this class belong, the upper half of the expanded portion of the occipital bone, the parietal, and frontal bones, the squamous portion and tympanic ring of the temporal bone, the nasal, lachrymal, malar and palate bones, the upper and lower jaw, the *vomer,* and apparently, the internal lamella of the pterygoid process of the sphenoid, and the *cornua sphenoidalia.* The blastema of these bones, which differs from that of the primary bones, in its being successively developed in a membranous matrix, simultaneously with the process of ossification, not existing previously in any considerable quantity, presents essentially, exactly the same conditions as that of the periosteal layers, and is also ossified in precisely the same way.

[The notion that certain cranial bones, in man and the Mammalia, are not developed from cartilage, is by no means new, although the morphology of the question was first established by Rathke, Reichert, Jacobson, and myself; and its histology by Sharpey and myself. But with respect to the latter subject, a controversy still exists as to the true nature of the ossific blastema (as also, of that of the

periosteal layers),—whether it be a kind of connective tissue, as I believe, or a sort of cartilage, as Reichert and A. Bidder assert, with respect to which more will be found in my 'Mikroskop. Anat.,' pp. 374, 375.]

§ 107.

The secondary cranial bones, all, in the first instance, commence in the form of a minute, elongated, or rounded, osseous nucleus, consisting of a portion of fundamental substance or matrix, with a few lacunæ, and which is surrounded by a small quantity of soft blastema. How this nucleus originates, has not yet been observed, although from the way in which its growth proceeds, it might be assumed with certainty, that shortly previous to its first appearance, a minute lamella of the soft blastema is formed in the situation of the future nucleus, which lamella spreading from a single point, becomes ossified by the addition of earthy salts and the metamorphosis of its cells. The primary point of ossification having thus appeared, for instance in the parietal bone, its growth advances simultaneously with the horizontal extension of the membraniform blastema, in such a way that a delicate lamina composed of reticulated osseous spicules is shortly produced, from which, slender rays stretch out into the still unossified blastema (fig. 135). If this formation be examined more closely, it will be observed, that the individual bone-spicules originate in the membranous blastema, by the ossification of its elements, and, that to a certain extent, the latter is absorbed in the spaces occupied by the spicules, remains of it being left in the interstices; and moreover, that the formation of the osseous elements pro-

Fig. 135.

Fig. 135. Parietal bone of a fourteen-weeks old fœtus, × 18 diam.

ceeds exactly in the same way, that it does in the periosteal layers; the rays of bone as they extend further into the soft blastema becoming softer and paler, and containing less earthy matter, whilst their cells become more and more like the soft formative cells, till, at last, the spicules lose all distinct limitary outline, and are lost in the blastema. At first, the growth of these bones proceeds in a superficial plane only, the rays, as they extend and become connected by transverse branches continuing to add to the size of the original, reticulated lamella, which, however, shortly begins to increase in thickness by the deposition of layers upon both sides of it; the different portions, also, in proportion to their age becoming more and more compact. The formation of the thickening layers is to be referred to the periosteum, which is found on the surfaces of the secondary bones, very soon after their formation has begun, being developed either from their original blastema, or from the contiguous tissues (perichondrium of the primordial cranium, muscular and tendinous coverings), and proceeds exactly in the same way as in the periosteal layers of the primary bones; that is to say, on the inner side of the periosteum, a soft blastema is deposited, which gradually ossifies, from the bone outwards, without its ever being cartilaginous (fig. 136). In this way are now formed, chiefly on the outer, but also on the inner surface of the primary osseous lamella, and proceeding outwardly from it, successive, new laminæ, in consequence of which, the rudimentary bone continually increases in thickness. All these

Fig. 136.

Fig. 136. From the inner surface of the parietal bone of a new-born child, × 300 diam.: *a*, bone with lacunæ, still pale-coloured and soft; *b*, border of the same; *c*, ossifying blastema with its fibres and cells. *B*, three of these cells, × 350 diam.

new lamellæ, like the primary one, are at first perforated by reticular openings, and the various sized, roundish or elongated interstices communicate with those of the previously and subsequently formed layers, so that the secondary osseous nuclei, like the periosteal layers, are, from the first, penetrated by a network of canals, which, as in those layers, in part at least, soon present the appearance of Haversian canals. At first, filled only with a soft blastema, the remains of the plastic material of the various lamellæ, these spaces, in consequence of the advance of ossification in their interior,—which sometimes takes the form of bridges stretching across them, sometimes of a deposit on their walls,—become more and more contracted. Ultimately, some are entirely closed, whilst others are converted into true vascular canals, the vessels being developed from their contents, which are composed during this time of medulla-cells, and communicating with those of the *periosteum*. When the bone has arrived at this stage, its subsequent changes are readily followed. It continues to increase in breadth and thickness by the constant addition of new blastema on its edges and surfaces, until it has attained its typical form and size, and at the same time, by the solution of its compact substance, additional spongy tissue (or even large cavities), is formed in its interior, so that eventually, like bone developed from cartilage and periosteal layers, it presents, externally, compact substance with Haversian canals; and internally, medullary spaces (cancelli), although with distinct secondary deposits.

[The secondary cranial bones ossify, in part, earlier than the primary, and mostly with only a single nucleus. The soft blastema out of which they are formed, and which, so long as the bones continue to grow, is to be found on their surfaces and edges, does not, like cartilage, grow independently with them, but is developed by degrees, from a plasma successively secreted from the vessels of the *periosteum*, the two lamellæ of which are conjoined at the margin of the ossifying plate. The cells of this plasma, the metamorphosis of which, as in the periosteal layers, cannot be followed in every particular, are elongated, measuring in man, for the most part, 0·006—0·01‴, and presenting granular contents

with oval nuclei of 0·0028—0·0048‴. Such of these cells as are destined for the growth of the bone in thickness, with the exception of those of the glenoid cavity of the temporal bone, never present the slightest resemblance to cartilage-cells, and, together with their matrix, invariably ossify without the appearance of any calcareous particles; those on the borders or extremities, on the contrary, may, as it appears, *subsequently*, take on the nature of true cartilage. The most striking example of this kind occurs in the condyle of the inferior maxilla, where, even during fœtal life, a thick cartilaginous layer is deposited, which so long as the growth of the bone continues, precedes its longitudinal growth, exactly like an epiphysal cartilage. I have noticed the same thing in the articular fossa of the temporal bone, where, however, the cartilage is less developed; at the angle of the inferior maxilla (in the Calf), and at the anterior extremities of each half of the same bone, which are connected by a semi-fibrous, semi-cartilaginous substance, corresponding very nearly with the *symphysis*. This fact loses much of the singularity which at first sight attaches to it, when we consider that *all cartilage is at first soft, and consists of common formative cells*. It is, consequently, only necessary, that the formative cells of the soft blastema of the secondary bones, should, at a certain period, pass through the same changes as those undergone by the formative cells of embryonic cartilage, in order to effect the production of cartilage in the bones now in question. Further investigation is required to show, whether cartilage of this kind also occurs as a supplementary addition to other secondary bones, and to what extent, in animals. Still, it may be noticed, that in asserting as I have done, that all ossifications from a soft blastema take place without the deposition of calcareous granules, this statement is only in part correct, because it is quite true, in many cases, that this sort of deposition does occur in them, though *never at an early period*, and, generally speaking, *but rarely*. The ossifying margin, moreover, in these cases is never abrupt, as it is in ossifying cartilage.

The ultimate changes of the secondary bones have not yet been closely investigated. Their mode of connection with each other, and also with primary bones by suture and coalescence, is tolerably well known. In the vault of the

cranium, for instance, as the primary ossific points first appear in the situation of the tuberosities of the parietal and frontal bones, the bones are at first placed widely asunder, and are connected merely by a fibrous membrane, the continuation of the periosteal lamella of each, and which is united on the internal aspect with the remains of the membranous cranium of the embryo, and with the *dura mater*. The bones then continue to grow towards each other, and at last, constantly advancing in the above-described continuation of the *periosteum*, come very nearly into contact at the frontal and sagittal sutures; there remains, however, for a long time, one large vacuity, in particular, between them,—the anterior fontanelle,—but which closes in the second year after birth; whilst at the same time, the bones, which, up to this period, adjoined each other with a straight line of juncture, send out interdigitating tooth-like processes, till ultimately, when their blastema is wholly consumed, they continue united only by the remains of the *periosteum* (the sutural cartilage, as it is termed, or better, the sutural ligament), but which also is capable of becoming ossified sooner or later, and, indeed, invariably first on the inner aspect of the suture, where the tooth-like processes are very little developed. The changes of form in the entire bones during their development are very remarkable, and have hardly been attended to. If a parietal bone, for instance, of a fœtus or new-born child, be compared with that of an adult, it will be found that the former is much more curved, and in no way at all represents a piece cut out of the middle of the latter. The adult parietal bone consequently must have undergone a very important alteration in the curvature of its surfaces, and this, as mechanical conditions are out of the question, can only have been effected by an unequal deposition of bone internally and externally, in the middle and at the borders; or by deposition on the one side and absorption on the other. That unequal deposition does actually occur, is seen, for example, in the *juga cerebralia* and *impressiones digitatæ*, the *sulci meningei*, &c.; but it appears to me, that the whole matter cannot be understood, unless we assume that *local absorptions* also take place in certain situations. How otherwise can be explained the increase in breadth of the superior orbital ridge, the increase of distance between

the frontal eminences, even after the ossific union of the two portions of the frontal bone, the change of form of the lower jaw (the greater distance between the coronoid processes and the mental spine, the alteration in its curvature, the partial removal and renewal of the *alveolæ*), &c.? We have already seen, that in the other bones, also, something of the kind must be presumed to take place, and, consequently, cannot hesitate to admit it in the present case, although the particulars of the process be unknown. That this process occurs in the interior of the secondary bones has been already mentioned. The formation of the *diploë*, which becomes more evident in the tenth year, is to be referred to it, as is also that of the frontal sinuses, and *antrum Highmorianum*, which however does not take place till a later period.

I would further remark, that the secondary bones, so long as they are in a growing state, are much more vascular than afterwards, even exceeding, in this respect, the periosteal layers of the other bones; on which account their medulla, containing the multi-nuclear, enigmatical bodies, already referred to, is of a redder colour. The vessels enter these bones at innumerable points on the surface, and, in the different bones, run in vertical or horizontal canals. The latter is the case in the flatter bones, in which the vascular channels run principally in the longitudinal direction of the osseous rays proceeding from the primary point of ossification; and the former, in consequence of which the surface of the bone frequently presents an extremely delicate, millepore-like aspect, occurs in the thicker portions. A great many of these canals afterwards become obliterated, or, at all events, very much contracted, whence the surface of the bone is rendered smoother.

In conclusion to these remarks on the development of the bones, I will add a few words regarding their conditions at different periods. Valentin noticed the cartilaginous rudiments of the ribs in a human embryo 6‴ long. That of the cranium is distinctly recognisable in the sixth or seventh week, as well as those of the vertebral zone and that of the extremities; those of the extremities proper do not appear till later (in the eighth or ninth week). Ossification commences as early as the second month, first in the clavicles and lower jaw (fifth to seventh week), then in the *vertebræ*, the *humerus*,

femur, ribs, and the cartilaginous portion of the lamina of the occipital bone. At the end of the second, and beginning of the third month, ossification is apparent in the frontal bone, *scapulæ*, bones of the fore-arm and leg, and upper jaw; in the third month, in the rest of the cranial bones, with few exceptions, the metacarpal and metatarsal bones, and phalanges; in the fourth month, in the *ilium* and *ossicula auditûs;* in the fourth or fifth month in the ethmoid, the turbinated bones, the *sternum*, *pubis* and *ischium;* in the sixth to the seventh month, in the *os calcis* and *astragalus;* in the eighth month, in the *os hyoides*. At birth, the *epiphyses* of all the cylindrical bones are still unossified, with the occasional exception of those at the lower extremity of the *femur* and upper end of the *tibia;* and besides these all the carpal and the five smaller tarsal bones, the *patella*, sesamoid bones, and the last segment of the *coccyx*. After birth, up to the fourth year, the nuclei of these bones also make their appearance; but, in the *os pisiforme*, not till the twelfth year. The union of most of the *epiphyses* and processes with the *diaphyses* takes place, in part at the time of puberty, in part towards the end of the period of growth.][1]

[1] [Dr. Sharpey's discovery that certain bones of the skull are developed in the same manner as those layers which are formed under the periosteum in the long bones, has been a sort of apple of discord among histologists, and has produced a great variety of controversies not only among them, but among comparative anatomists; controversies whose heat has been somewhat increased, as we think, by a want of perception among the combatants, of the fact, that several totally distinct questions are involved. These questions seem to us to be the following, and we shall endeavour to consider them in detail.

1. Whether the tissue from which "secondary" bone proceeds is cartilage, or not?

2. Whether it is morphologically homologous with cartilage, or not?

3. Whether ossification takes place in it in the same manner as in cartilage, or not?

And as the result of the answering these:—4. Whether the differences between the two tissues are sufficient to constitute the basis of a classification of the bones, or not?

1. To answer this by saying with Meyer that every tissue which ossifies is cartilage, is simply to beg the whole question. Cartilage we hold to be distinguished from indifferent tissue, by the fact of its matrix containing chondrin. The substance which in the fœtus contains no chondrin, but will subsequently become a cartilage—though in common parlance it is very convenient to call it "fœtal cartilage"—is no more cartilage than the cartilaginous basis of a future bone, which might just as properly be called fœtal bone, is osseous tissue. There can be no question then, we

§ 108.

The *vital phenomena* exhibited in the *mature bones* are not, during the vigorous period of life, accompanied with any nota-

think, that Kölliker is in the right, as against Reichert, Meyer, and others, when he says that secondary bone is not developed from cartilage, and that, in this respect, it may be distinguished from primary bone.

2. Though this matrix of secondary bone, however, is assuredly not cartilage, it is another matter whether it is, or is not, morphologically homologous with cartilage. To arrive at any just conclusion on this head, it is necessary to understand the precise structure of this tissue, which Messrs. Tomes and De Morgan have been the first to point out: "If attention be directed to the part furthest removed from the bone, it will be seen that the membrane-like mass is composed of oval cells with slight prolongations from the extremities, which are frequently arranged in the form of bands of fibrous tissue. Dr. Sharpey has observed that the membrane into which the bone extends is like fibrous tissue in an early stage of development; and this observation is strictly true when confined to the part indicated, but the analogy ceases [? Eds.] as we extend our examination towards the bone. Here, in the place of cells with elongated processes, or cells arranged in fibre-like lines, we find cells aggregated into a mass, and so closely packed as to leave little room for intermediate tissue. The cells appear to have increased in size at the cost of the processes which existed at an early stage of development and formed a bond of union between them. Everywhere about growing bone, a careful examination will reveal cells attached to its surface, while the surface of the bone itself will present a series of similar bodies ossified. To these we propose to give the name of *osteal* cells, as distinguished from lacunal and other cells. In microscopic characters, the osteal cells closely resemble the granular cells of temporary cartilage; so closely, indeed, that the latter, when detached from the cartilage, could not well be distinguished from them. They are, for the most part, spherical or oval in form, and lie on the surface of the growing bone in a crowded mass, held together by an intervening and apparently structureless matrix. Here and there we find a cell which has accumulated about itself an outer investment of transparent tissue, and has, in fact, become developed into a lacunal cell destined to become a lacuna" (l. c., p. 23).

The tissue, then, from which secondary bone immediately proceeds, is composed of a homogeneous matrix, in which, corpuscles, identical with the cartilage-corpuscles, are imbedded (see fig. 136 *A*, 1, *a*): it is therefore identical, as Dr. Sharpey described it, with young connective tissue; and as we have seen above (note, § 101), and as the authors state, with fœtal cartilage. Though not cartilage, therefore, it is homologous with it (as is, indeed, admitted by Professor Kölliker); a fact which is still more strongly evidenced by the transition of cartilage into a similar tissue, at its edges (Tomes and De Morgan, l. c., p. 24), which may readily enough be observed, and which has been particularly shown by Reichert to occur between the primary and secondary bones of the skull ('Zur Streitfrage über die Gebilde der Bindesubstanz, über die Spiralfaser und über den Primordial-Schädel,' Müller's 'Archiv,' 1853).

Now it seems to us that a tissue which is identical with the embryonic form of

ble or active morphological changes. It is true that, during this period, some of the processes above considered go on—such

cartilage, which passes into adult cartilage, and differs from cartilage only in the absence of chondrin (in which respect ossified cartilage agrees with it),—is in a morphological point of view homologous with cartilage.

3. With respect to the third question,—Sharpey and Kölliker are of opinion that the deposit of calcareous matter and the formation of lacunæ take place in the same manner as in cartilage, *i. e.* that the calcareous salts are deposited evenly through the matrix, leaving spaces round the corpuscles or "nuclei," from which the canaliculi are subsequently developed by resorption. Messrs. Tomes and De Morgan, on the other hand (see passage cited above), maintain that secondary bone differs from primary, in so far as certain of the corpuscles—"osteal cells,"—"arrange themselves side by side, and together with the transparent blastema in which they lie, become impregnated with ossific matter, and permanently fused with the bone-tissue with which they lie in contact. By the linear arrangement of these osteal cells, lamination is produced. In the case of new laminated bone, the cells are simply ossified without arrangement. Lying amongst the osteal cells will be seen *some which have accumulated around them a quantity of tissue which forms a thick investment to them;* they then become granular, and take on in every respect the characters of a lacunal cell. These are found deposited at intervals along the line of ossification, and becoming blended with the general mass, the granular cell remaining as a lacuna, and sending out processes in all directions" ('Abstract in Proceedings of Royal Society').

We must confess that all we have seen leads us to believe that the former of these accounts is correct. We have never been able to find evidence of any of the corpuscles becoming converted into "osteal cells," and we believe, for the following reasons, that this process does not take place. In examining the growing Haversian canals in Man, and particularly in the Calf (fig. 136 *A*, 1), we have very frequently found the innermost layer transparent, glassy, and structureless—exhibiting nothing but the corpuscles (*d*) lying in lacunæ without canaliculi. This layer would be as much as $\frac{1}{2000}$th of an inch thick; in the layer (*c*) immediately external to it, however, the "osteal cells" were exceedingly well marked. The inner layer looked like smooth ice, and the outer like ice which had cracked into innumerable tolerably even portions—but these cracks were by no means produced by the canaliculi, which, as yet, were hardly at all developed. Now it seems clear that if the "osteal cells" were produced by the calcification of certain of the corpuscles, they ought to be more obvious in the young, inner layer, than in the outer; whereas just the reverse occurs. The fact stated by Messrs. Tomes and De Morgan, that lamination is less obvious in young than in old bone, tends to exactly the same conclusion. Again, if the granular substance between the lacunæ were composed of calcified corpuscles—"osteal cells,"—the action of acids ought to bring them out as strongly as it does those of the lacunæ; whereas neither in young bone nor in old can anything of the kind be seen.

With respect to the lacunæ, again, we have the same remarks to make as when speaking of cartilage. We have never been able to find any trace of the development of the corpuscles (granular cells) into lacunæ. As to the tissue which accumulates round them and forms an investment, we have frequently observed the appearance

as the enlargement of the sinuses in the cranial bones, of the points of insertion of muscles and ligaments, and of the vascular

described; but this investment was nothing but the clear, often homogeneous, calcareous matter, gradually encroaching on the matrix and inclosing the corpuscles.

We consider, then, that the process of ossification in primary and secondary bone is identical; the deposition of the calcareous matter in granules or as a homogeneous infiltration, being of no constancy or importance. In each case the deposit takes place in the matrix, and leaves spaces (lacunæ) round the corpuscles (nuclei, granular cells). Subsequently, the canaliculi are developed in the matrix by a process of resorption; while their walls and those of the lacunæ may or may not become chemically differentiated from it. At the same time, the matrix may or may not break up into laminæ and "osteal cells" or granules. Its variability in this respect is neither more nor less remarkable than the greater or less fibrillation of the corresponding element of connective tissue, or than the inconstancy of the disposition of the cleavage lines of the same element in striped muscle.

Fig. 136 *A.*

As little is any line of demarcation to be drawn between primary and secondary bone as regards the tissues from which they proceed. Indifferent tissue, in which calcareous matter is deposited at once, is the basis of secondary bone; an identical tissue—in which to serve a temporary purpose chondrin is deposited, being subsequently withdrawn and replaced by calcareous salts—is the basis of

Fig. 136 *A.* 1, wall of Haversian canal from the metatarsal bone of a Calf; *a*, structureless matrix; *b*, homogeneous calcareous deposit replacing it and forming the inner lamina of the canal; *c*, more external lamina broken up into "osteal cells;" *d*, corpuscles; *e*, lacunæ: 2, ossifying cartilage of the Skate, for comparison; letters as above. Both × 600.

channels; but a more extensive new formation of bone, whether periosteal or in the Haversian systems, together with a simultaneous and more considerable absorption, never occurs in them. It was formerly believed that the coloration of the bones of adult animals by madder, proved that deposition of bone substance continued to take place even in them, it being assumed that newly forming osseous tissue only became coloured; but since it has been shown, that bones already formed were likewise coloured by the same agent, and that coloured bones in the adult did not lose their colour (Brullé and Huguény), this view becomes untenable. Whether in the perfect bone a change, if not of the elementary parts, but still of the atoms, takes place, the same external figure remaining, is another question, for the solution of which microscopy affords no facts. This much is certain, that the organisation of bone is such, that notwithstanding the rigidity of their structure, they are in the most general and most intimate relation with the nutritive plasma of the blood. In every situation where the osseous tissue is in connection with vessels, as on the external surface, in the walls of the medullary cavities and cancelli, and those of the Haversian canals, millions of closely crowded minute openings exist. These convey the blood-plasma, by means of the *canaliculi,* into the lacunæ lying nearest to the surfaces mentioned, from which it is then conducted by wider canaliculi to the more distant lacunæ, as far as the outermost layers of the Haversian lamellæ, and those laminæ of the great lamellar system which are most remote from the vessels. When the enormous number of the canaliculi and their multifarious anastomoses are considered, it must be allowed that no tissue in the human body is better provided for in respect of the distribution of the blood-plasma, whilst in scarcely any other is the direct conveyance of the fluid to the most minute particles more immediately necessary than in it. There can be no doubt that the fluids, which this "plasmatic vascular system" (Lessing) of the bones, obtains from the blood-vessels, probably somewhat modified by the influence of the nucleus

primary bone. And this paragraph may serve as an answer to the fourth question. If it be correct, we cannot imagine that any distinction of the bones into primary and secondary, upon the ground of their development or non-development from cartilage, can be other than arbitrary.

which, as I have before endeavoured to show, is still retained in every lacuna, are most indispensably requisite for the maintenance of the bone; for we see, that when the supply of blood to a bone is impeded by the destruction of the periosteum or of the medulla, by ligature of the vessels of the limb, or by obliteration of the periosteal vessels by pressure from without (aneurism, tumours), necrosis of the parts involved certainly ensues, and can scarcely in any case be altogether obviated by the collateral circulation which actually exists also in the bones (*vid. supra*). On the other hand we are scarcely, at present, in a condition to say, how the circulation of the plasma in the bones is carried on, though its movement to and from vessels (perhaps from the arterial, through several lamellar systems to the venous) must probably be assumed; or what special changes in the course of the nutrition of bone take place; with the latter in particular we are unacquainted, because the chemical investigation of these changes, and especially of the organic products of decomposition, is still altogether imperfect.

That the osseous tissue is in a state of constant, and indeed very energetic molecular change, is evidenced not only in its various morbid conditions, but also by the alterations it undergoes in old age. These alterations consist more especially in the disappearance of entire portions of the bones, either externally or internally; of the former, an instance is afforded, in the entire removal of the alveolar processes of the jaws, and the latter is seen in the greater porosity and fragility of every kind of bone, such as the cylindrical bones and those of the cranium, in the enlargement of the vascular openings (*vertebræ, apophyses*), and in the greater roughness of the surfaces of the bones. This senile atrophy of the bones may also be attended consecutively with an internal addition of bone-substance, a *sclerosis* as it is termed, as in the flat bones of the cranium, in consequence of which, in direct contrast to the phenomena elsewhere presented by senile bone, the *diploë* disappears, its cancelli becoming filled up by new osseous tissue, whilst the venous spaces and *foramina emissaria* are obliterated and the entire bone rendered heavier.

With this abundant vascular supply, and certainly not sluggish molecular change, it cannot be surprising that the bones should be so richly furnished with *nerves*, the *principal*

function of which appears to me to consist in the regulation of the conditions of the vascular system, by their conveying to the central organ (spinal chord) through the sensitive fibres intelligence of the state of the vessels, of the quantity of nutritive fluid in the bone, and probably also of the modus of the molecular change going on in themselves, and by means of the motor elements their bringing a reflex influence from it, to the arteries and veins which are manifestly furnished with contractile fibres. These unconscious and involuntary alternations of influence of sensible and motor filaments, are, as it appears to me, the most important phenomena of the innervation in bones, as well as in all other organs, the nerves of which are not constantly in relation with the external world, and make it intelligible, why it is, that no organ, containing nerves and vessels at all, possesses nerves of only one kind. It is not, however, by this, intended to imply that the nerves of bones do not convey conscious perceptions; it is possible that, through them, we obtain a certain degree of knowledge of the processes going on in the bones, of the degree of fulness of the vascular system, the mechanical influences to which they are exposed from without in the movements caused by the action of the muscles, the weight of the body or of external objects, in lifting weights, mastication, &c.; but in any case this knowledge would be very indeterminate, and the sensation excited not definitely localised, being confused in the general feelings of fatigue, effort, or relaxation. On the other hand it is quite certain that the bones, in man, in many diseases, and in consequence of mechanical injury, afford pain, which latter fact has also been frequently noticed in animals, at all events, upon irritation of the larger nervous trunks of the *diaphyses*. In man the *apophyses* in particular, and the vertebral and cranial bones, seem readily to become painful, which is explained by the considerable number of nerves immediately in the spongy substance. The compact substance on the other hand might probably be regarded as scarcely obnoxious to pain; as, for instance, in resections, but not so perhaps the periosteum, which less from its own nerves than as the vehicle of those of the bones before they enter their destination, must naturally be affected in the same way that they are. Whether the nerves of the bones through which, perhaps, the conscious

perceptions, but in any case the painful impressions are conveyed, be identical with those through which the reflex actions, above referred to, are carried on, is not determined; but, looking at the origin of most of the bone-nerves from the cerebro-spinal nerves, such an opinion might perhaps be maintained, it being premised that the connections of the nerves with the brain are to be regarded as less intimate than in the case, for instance, of the cutaneous nerves. I would, in addition, call attention to the remarkable occurrence of nerves in the cartilage of the *septum narium* in the Calf, although I am unable to say anything more with respect to their nature than with regard to that of the nerves of bone.

[On the subject of the numerous pathological changes which occur in the bones, only some brief remarks can here be made. Fractures readily unite, under but moderately favorable circumstances, by true bone-substance, which, in the cylindrical bones of animals is preceded by the formation of a true cartilage, a fact of which I and others are satisfied; whilst, according to Paget, this rarely appears to be the case in man. In the spongy bones, in fractures within the articular capsules, and under unfavorable circumstances, the fractured ends frequently unite merely by a fibrous callus, a sort of articulation being formed between them. After loss of substance the osseous tissue is readily regenerated; and it is the periosteum especially, which, in this case, as in the growth of a bone in thickness, plays the principal part in the restoration; of course by means of the exudation poured out from its vessels. In animals, entire bones of the extremities, and ribs are regenerated, pretty nearly in their original figure, not only when the periosteum has been saved, of which many examples are exhibited in Heine's collection in Würzburg, but even after entire excision with the periosteum, a rudiment of the bone is reproduced (Heine). In man also, a good many instances have been afforded of the reproduction of entire bones, such as the lower jaw, the ribs, the scapula (Chopart); and the cases of isolated,—in some instances large, portions of bone being so regenerated are very numerous. It is especially the diaphyses, which are readily replaced, when they have been lost in one way or another, less frequently the spongy bones and spongy

parts of bones, and those of the cranium; in the latter, however, openings made by the trephine are in many cases filled up, instead of fibrous membrane, with isolated patches of bone, or even with an entire piece of bone; in fact, trephined portions of bone have united exactly in the same way as has been observed to take place with portions of bone half cut off (Pauli). *Hypertrophy* of bone assumes the most various forms, all of which may be reduced under two principal types: 1. deposits on the surface, or external *hyperostoses*, which are formed chiefly from the *periosteum;* and 2. internal or *scleroses*, which consist in the filling up of the medullary cavities and Haversian canals with new bone, and these two forms may occur either separately or combined. The former takes place in inflammations of the periosteum, either idiopathic or in connection with cancer, *arthritis*, *syphilis*, &c., the latter not only consecutively in old age, but also in *rachitis*, *osteomalacia* and *syphilis*. With respect to the microscopic conditions of these growths, Virchow deserves the credit of having distinctly indicated ('Archiv, f. pathol. Anat. I,' p. 135), that the bony growths or osteophytes on the cranium are formed by a direct ossification of connective tissue without any preliminary development of cartilage, which is also undoubtedly the case in the filling up of the losses of substance in the *cranium*, in regeneration proceeding from the periosteum, and in most cases of *sclerosis*. The newly formed osseous substance is sometimes like the normal (many exostoses), sometimes more dense, with small vascular spaces and large irregular lacunæ. *Atrophy* of the bones is shown in their disappearance in totality in consequence of chronic diseases, paralysis, *anchylosis;* or in *rarefaction* of the osseous tissue analogous to senile atrophy, in *syphilis*, *lepra*, mercurial cachexy, paralysis, &c. *Death* of bone (*necrosis*) is observed in cases where the periosteum has been destroyed; in inflammations of that membrane and of the bone, &c., for the most part attended with an excessive growth of the remaining sound parts. Peculiar morbid conditions exist in *osteomalacia* and *rachitis*, but in neither of these diseases have microscopical researches afforded anything worth mention here, except what has been made known by H. Meyer and myself (ll. cc.) with respect to ossification in *rachitis*. In this case I have found: 1. that in the disproportionately large

epiphysal cartilages, the layer of the ossifying cartilage-cells (those disposed in rows), measured, instead of $\frac{1}{2}'''$, $2—5'''$; 2. that the ossifying border is toothed, owing to the circumstance that the cartilage and bone interlace in various ways; 3. and lastly, that in decidedly rachitic bones, the deposition of calcareous granular particles is wanting, and the cartilage-cells almost invariably, shortly before the matrix, and also without any appearance of calcareous granules, are metamorphosed into bone-cells, on which account the formation of the latter can, in no case, be so well studied as in these bones (*vid. supra*). *Accidental cartilage- and bone-formations* are very frequent. The former tissue is met with, notwithstanding that it is incapable of regeneration, and that wounds of it heal only with a fibrous tissue, more rarely with bone (ribs), in very many organs (bones, mammary glands, parotid, testicles, lungs, and skin) forming what is termed *enchondroma;* moreover, as a new covering on the osseous growths, at the border of the worn articular ends of bones (Ecker). The latter is seen in ossifications of the permanent cartilages (ribs, *larynx, epiglottis,* very rarely) of tendons (*exercir-knochen,* for example), in the *dura mater* and *arachnoid* (Miescher, Rokitansky), in the eye (Valentin), in the ovary, in fibrous membranes (*membrana obturatoria*), in *enchondroma,* in fibrous and carcinomatous growths, and in the lungs (Mohr's cysts containing hair). Even in these cases the osseous tissue does not essentially differ from the normal, and it is formed, sometimes from a cartilaginous, sometimes, and in fact mostly, from a soft blastema (Virchow, l. c. p. 137).

In investigations relating to the structure of bone, good sections are, above all things, requisite. With a fine saw, thin slices are made, which are ground with water upon a smooth stone with the finger, or with a second smaller stone, for some minutes (5—10), until they are rendered uniformly transparent. The sections are then cleaned, and (the fat, if they contain any, being removed by ether) may be employed, being wetted with water, for the study of the Haversian canals and disposition of the lacunæ; and with turpentine, for that of the various lamellar systems. The lacunæ and their prolongations, which, in sections, are dark and very distinct, owing to their being filled with air, are completely filled by thin turpentine,

so that the latter in great part, and also the former, are very frequently rendered invisible; the same thing happens in water and thicker turpentine, though less rapidly, whence, before these agents have produced their effect throughout, many of the lacunæ and canaliculi are beautifully shown. If it be desired to preserve the lacunæ and canaliculi permanently visible, it is best to polish a thin section, by rubbing it between two glass plates. It may then be examined without the addition of fluid, and presents as perfect figures as those represented in figs. 115—117. The grinding of the bone with oil is not to be recommended, because the lacunæ then become filled with the oil, and even after thorough treatment with ether can seldom be rendered distinct. Next to sections of bone, the investigation of the bone-cartilage is the most worth while. This tissue is prepared by the treating of bone in the cold, with diluted hydrochloric acid (1 part acid, 10—20 water), until the fluid, which is to be frequently changed, no longer affords any precipitate with ammonia; for which purpose, in small fragments of bone, some hours, in entire bones several days, are required. From the cartilage thus obtained, sections are now to be made with a sharp knife in all directions, suitable chiefly for the study of the Haversian canals and lamellæ, which may even be raised from the surface. The lacunæ, also, are still visible; their prolongations or canaliculi appear as fine streaks, and their nuclei are seen without further trouble, especially also after treatment with potass, or in cartilage which has been half dissolved by boiling in water. After longer maceration in hydrochloric acid, the lacunæ even become isolated, as stellate bodies with delicate walls, or, in the *cementum* of the horse's tooth, as structures corresponding to the former cartilage-cells. After long softening of bone-cartilage in water, the lamellar systems of the Haversian canals become more or less completely separated, presenting the appearance of short, coarse fibres among the larger lamellæ (Gagliardi's *claviculi*). If bone be exposed in a platinum capsule to a strong white heat, the organic parts burn away, the bone becoming at first black, and ultimately perfectly white; and if due care be taken, the earthy constituents are left, completely retaining the original figure of the bone. Preparations of this kind are proper for the study of the laminated

structure of the compact substance and of the lamellar systems of the Haversian canals, which, in this case also, sometimes appear isolated, as in macerated bone. For the microscopic examination of the inorganic constituents of bone, sections are subjected to heat on platinum foil, but they must be very thin, as they afterwards become more opaque, and, on account of their fragility, except in minute fragments, do not admit of being ground thinner (Bruns); or sections may be boiled in caustic potass. In either case, the lacunæ are seen distinct, and *empty*, with the beginnings of the canaliculi, in a finely granular matrix. The natural condition of the lacunæ is readily seen in perfectly recent bone, in thin sections or lamellæ; as, for instance, in many parts of the bones of the face. In recent bone, also, the vessels may be studied, naturally injected, and with the microscope, being thus, far fitter for the purpose than when injections, which often fail, have been practised, and for the closer examination of which, moreover, the bones must afterwards be macerated in hydrochloric acid, and preserved in oil of turpentine. The nerves of the bones may be seen by the naked eye, on the nutritious arteries of the larger cylindrical bones, and readily, by the microscope, on the smaller vessels; those of the periosteum must be studied after the membrane has been rendered transparent by caustic soda or acetic acid. The costal and articular cartilages are the most suitable for the study of cartilage, the membranes of the cartilage-cells being evident, sometimes without any addition, sometimes after that of acetic acid or soda, which render the matrix transparent. The development of bone may be investigated in a cylindrical bone, and in the parietal bone; the formation of the lacunæ, *in specie*, in rachitic bones, and in the osseous surfaces of the *symphyses* and *synchondroses*.]

Literature.—Besides the works cited in §§ 22 and 25, are to be noticed, F. Bidder, 'Zur Histogenese der Knochen,' ('On the Histogenesis of Bone'), in Müller's 'Arch.,' 1849, p. 292; E. v. Bibra, 'Chemische Untersuchungen üb. die Knochen und Zähne des Menschen und der Wirbelthiere,' ('Chemical Researches on the Bones and Teeth of Man and the Vertebrata'); Schweinfurt, 1844; Vötsch, 'Die Heilung der Knochenbrüche per primam intentionem,' ('Union of Fractures, &c.'); Heidelberg, 1847; Kölliker, 'Ueber

Verknöcherung bei Rachitis, u. üb. den Bau der Synovialhäute,' ('On Ossification in *Rachitis,* and on the Structure of the synovial Membranes'); 'Mitth. der Zürich. nat. Gesellsch.,' 1847, p. 93; Rokitansky, 'Beiträge zur Kenntniss des Verknöcherungsprocesses,' ('Contributions to a knowledge of the process of Ossification'), in the 'Zeitschrift der Wiener Aerzte,' 1848, p. 1; A. Krukenberg, 'Zur Lehre vom Röhrensysteme der Zähne und Knochen,' ('On the Tubular System of the Teeth and Bones'), in Müller's 'Archiv.,' 1849, p. 403; H. Meyer, 'Der Knorpel u. seine Verknöcherung ('Cartilage and its Ossification'), in Müll. 'Archiv.,' 1849, p. 292; Virchow, in 'Verhandl. der Würzb. phys. med. Ges.,' vol. i, No. 13; Robin, 'Observations sur le développement de la substance et du tissu des os,' in 'Mém. de la Société de Biologie,' 1850, p. 179; Brullé and Huguény, 'Expériences sur la développement des os dans les mammiféres et les oiseaux, Ann. d. Sc. Nat.,' 1845, Nov. p. 283; Flourens, in 'Ann. d. Sc. Nat.,' 2 série XIII, 103, ibid. XV, p. 202, ibid. 1845; Aout, p. 105, and Déc. p. 358; 'Compt. rend.,' T. XIX, p. 621; all his observations collected in 'Théorie expérimentale de la formation des os,' Paris, 1847-8, avec 7 pl.; Beck, 'Abh. üb. ein. in Knochen verlaufende Nerven,' Freiburg, 1846; Kölliker, 'Ueber die Nerven der Knocken,' ('On the Nerves of Bone'), in Wurzb. 'Verhandl.,' I; Luschka, 'Die Nerven in der harten Hirnhaut,' ('The Nerves in the *Dura mater*'), Tübingen, 1850: and 'Die Nerven des Wirbelcanales und der Wirbel,' ('Nerves of the vertebral Canal and of the Vertebræ'), Tüb. 1850.

OF THE NERVOUS SYSTEM.

§ 109.

The *nervous system,* regarded in the more general anatomical sense, constitutes a connected whole, consisting of two principal masses—the *spinal cord* and *brain,* and of numerous cords —*nerves*—extending from them to almost all the organs of the body. The two former— or the *central nervous system,* the

central organs, are to be regarded not merely from an *anatomical* point of view, as affording origin to the nerves, but, also, in a *physiological* sense, as excitors of the movements, and seat of the sensations, as well as of the mental or psychical actions, and consequently as belonging to a higher or governing order of parts, whilst to the latter must be ascribed more of a ministerial office—the communication of the contractions and sensations. This mode of regarding the two divisions of the nervous system, however, is only partially correct, because, in the first place, in the central organs, as in the nerves, very many subordinate parts exist; and, secondly, because in the peripheral nervous system, the so-termed ganglia, physiologically and anatomically, represent central organs. The older division also of the nervous system into *animal* and *vegetative,* after the observations of recent times, can no longer be maintained; and the latter,—the sympathetic or ganglionic nervous system, can only be regarded as a portion of the peripheral system, though undoubtedly peculiarly constituted.

ELEMENTS OF THE NERVOUS SYSTEM.

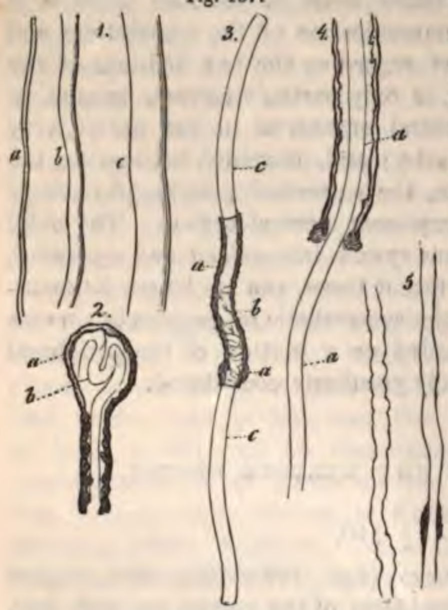
§ 110.

The *nerve-tubes* or *fibres* (figs. 137—139), also termed *primitive tubes,* or *primitive fibres* of the nerves, are soft, fine, cylindrical filaments, having a diameter of 0·0005—0·01‴; they constitute the principal part of the nerves and of the white substance of the central organs, although they are not wanting in the greater part of the grey substance of the latter and in the ganglia. When examined in the recent state and by transmitted light (fig. 137) they appear as clear as water, transparent, and with simple dark contours; by reflected light—glistening, opaline, like fat, in larger quantities together, white, and for the most part their appearance does not indicate that they are composed of different constituent parts. But it is readily seen upon the application of various methods, that they consist of three, entirely distinct, component structures, viz.: of a delicate coat, and a viscid fluid, in the centre of which is a soft but elastic fibre.

The *coat,* or *sheath* of the nerve fibres (limitary membrane,

Valentin) (fig. 139, 1, 2, 3, 4, *a*) is an excessively delicate, flexible but elastic, perfectly structureless and transparent membrane, which, in quite unaltered nerve fibres, except in certain situations, is altogether invisible. But on the application of suitable reagents, at least in the thicker fibres of the nerves and of the central organs, it comes readily into view, corresponding, in its chemical characters, in all essential particulars with the sarcolemma of the muscular fibres. In the finest fibres of the peripheral, as well as of the central nervous system, the existence of this membrane has not yet been demonstrated, and it must consequently, for the present, be left undecided whether these fibres possess sheaths or not.

Fig. 137.



Within the structureless sheath, lies the *nerve-medulla*, or pulp, ("medullary sheath," Rosenthal and Purkinje, "white substance," Schwann), (fig. 137, 3, *b*, fig. 139, 3, 4, *b*) in the form of a cylindrical tube, closely and exactly surrounding the central fibre. In the recent nerve-fibre this substance is perfectly homogeneous, fluid, but viscid like a thick oil, and, according to the light by which it may be viewed, transparent and clear,

Fig. 137. Nerve-fibres, × 350 diam. 1, from the Dog and Rabbit, in their natural condition; *a*, fine; *b*, of medium thickness; *c*, coarse fibre from the peripheral nerves: 2, from the Frog, with the addition of *serum; a*, drop of the contents expressed; *b*, axis-cylinder within the drop, continued into the tube: 3, from the spinal cord of Man, recent, with serum added; *a*, sheath; *b*, medullary sheath with double contour; *c*, axis-cylinder: 4, double-contoured fibre from the fourth ventricle in Man; the axis-cylinder, *a*, projecting and visible within the fibre: 5, two isolated axis-cylinders from the cord, one undulated, the other of unequal thickness, with some medullary substance attached to it.

or whitish and pearly, and it is obviously to it that the peculiar glistening appearance of the nerves is due. The nerve-pulp, is rapidly and invariably altered by the application of cold water, of most acids, and of many other reagents, the change consisting principally in a coagulation of it, which takes place gradually from without to within, sometimes involving the entire thickness, sometimes only its outermost layer. In the latter case, are produced the well-known nerve-fibres with double contour lines (fig. 137, 2, 3, 4), or in which the medullary sheath is, externally, coagulated to a greater or less extent, remaining fluid internally; in the former case, with the contents apparently wholly grumous and opaque (fig. 138). The coagulated nerve-medulla, in fact, seldom appears homogeneous, but most generally grumous, granular, and as if composed of separate, irregular, larger and smaller masses, and, upon the application of acetic acid, as if formed of minute, separate, or reticularly united rods. The nerve-pulp is also altered very readily by pressure. It sometimes escapes from the ends of the tubes, or from hernial protrusions or ruptures of the sheath, forming larger or smaller drops of every imaginable shape, regularly spherical, clavate, fusiform, cylindrical, filamentary, or of the most bizarre figures, which likewise coagulate either on the surface merely, or throughout, and thence, like the nerves, appear with a double contour, or half or wholly grumous. But, within the fibres also, its structural conditions alter, for, instead of being continued through them as before,—as a cylinder of uniform size,—it accumulates in places into larger masses. In this way are produced the frequently described, *varicose nerve-*

Fig. 138.

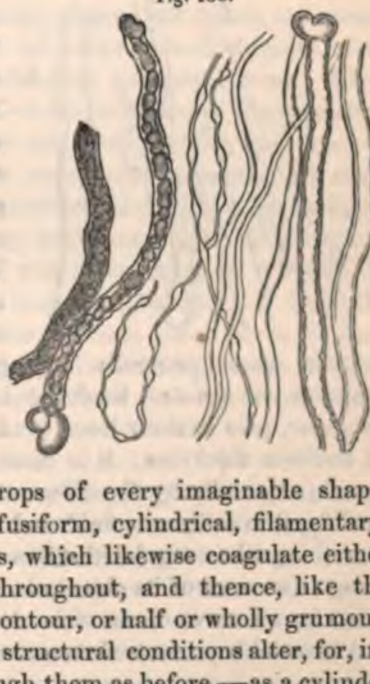


Fig. 138. Nerve-tubes of Man, × 300 diam.: four fine, two of which are varicose; one of medium size with simple contours; and four thick, two of which have double contours, and two, grumous contents.

fibres (fig. 138), in which the medullary sheath presents sometimes, minute moniliform enlargements, sometimes, various sized, irregularly distributed nodosities, or even, in places, complete interruptions. All these forms, in which the sheath frequently participates, but in which the central fibre takes no part, arise artificially, and are developed most readily in the finer fibres with more delicate sheaths, such as are found in the central organs.

The *central* or *axis-fibre* of the nerve-tubes ("*primitive band*," Remak, *cylinder axis*, Purkinje, fig. 137, 2, 3, 4, 5. 139, 1), is a cylindrical or slightly flattened filament, which, in entire and unaltered nerve-fibres, is as little recognizable as the sheath, being surrounded by the pulp, and possessing the same refractive power, whilst it comes readily into view when the fibre is torn or treated with various reagents; and it may thus be recognised as a *constant structure*, sometimes in the interior of the fibre, and sometimes isolated. Under natural circumstances it is pale, most generally homogeneous, more rarely, finely granular or striated, bordered by straight or occasionally by irregular, pale contour lines, and it is, generally, everywhere of uniform thickness: it is distinguished from the medullary sheath, especially by the circumstance, that although soft and flexible, it is still, not fluid and viscous, but elastic and solid, something like coagulated albumen, with which it also appears to agree in most of its chemical characters. This axis-cylinder exists in all nerve-fibres without exception, even in the finest, and invariably presents the same characters, except only, that it

Fig. 139.

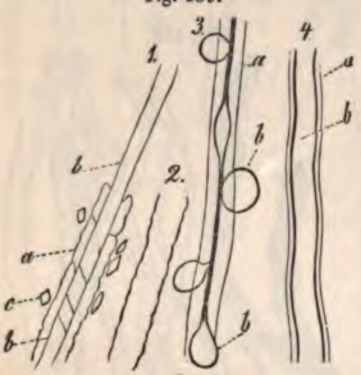


Fig. 139. Nerve-fibres, × 350 diam. 1, from the Frog, boiled with alcohol and acetic acid; *a*, sheath; *b*, axis-cylinder; *c*, crystals (fat ?): 2, isolated sheath of a Frog's nerve, boiled with soda: 3, from the floor of the fourth ventricle in Man, after treatment with soda; *a*, sheath; *b*, medulla flowing out in drops, the axis-cylinder is wanting (having been drawn out in the preparation), and the pale streak is medulla: 4, from the root of the *n. abducens* of Man, treated with soda; *a*, sheath; *b*, medulla, axis-cylinder not visible.

is sometimes thicker, sometimes more slender, according to the size of the fibre itself.

The *nerve-fibres* in which the three structures above described can be distinguished, and which we would designate as the *medullated* or dark bordered, constitute, it is true, the greater proportion of those existing in the body, but besides these there are still some forms requiring more particular description. These are the nerve-fibres in which there exists no trace of a medullary sheath; whilst they have an outer sheath and contents, sometimes identical with the axis-fibre of the other kind of nerves, sometimes similar but more clear. These *non-medullated* nerve-tubes occur, in the first place, as continuations to the other sort, where the latter are in connexion with nerve-cells; and also as more elongated, independent fibres, representing the so-termed processes of the nerve-cells of authors; and lastly, at the terminations of the dark bordered nerves. They may again be arranged in several sub-divisions, distinguished respectively by their having, or not having nuclei, and more or less transparent, more or less consistent contents. It must also be added, that the dark bordered fibres differ extremely—partly in respect of the delicacy or firmness of their structure, and partly in their diameter, which varies from 0·0005—to 0·01‴ or more, so that they may be distinguished into *fine* and *coarse, delicate* or *firm* fibres; from which it is evident that the nerve-fibres, notwithstanding their general tubular character, still differ pretty widely from each other in various respects.

[The *tunic* or *sheath of the nerve-fibres,* discovered by Schwann, in most nerves is brought into view with some difficulty. It is only rarely, as in the roots of certain cerebral nerves (those of the muscles of the eye for instance), and of the spinal nerves that it appears distinct from the contents; its presence however is, with certainty, and readily demonstrated by the aid of chemical reagents. When the nerves are boiled in absolute alcohol, soon after the removal of a considerable part of the fatty matter of the pulp, the sheaths become tolerably distinct, as dark boundary lines; and they are rendered remarkably and beautifully so by a short boiling in acetic acid, during which, the remaining contents of the nerve-sheaths, with the excep-

tion of the central fibre, escape from them, whilst at the same time numerous (fat) crystals (fig. 139, 1) are formed. When boiled in alcohol and treated in the cold with caustic soda, the nerve-fibres also exhibit the sheaths very beautifully, as pale, frequently undulating contours of the colourless, remaining contents; and when such fibres are boiled for a moment in caustic soda, numerous, elongated fragments of perfectly empty, somewhat swollen nerve-sheaths, are detached, which, from their delicacy, present a striking resemblance to the empty tubules of the *membrana propria* of the *tubuli uriniferi* (fig. 139, 2). The sheaths, however, are rendered most distinct by means of fuming nitric acid and the subsequent addition of caustic potass. In this case the fatty matter of the medullary sheath escapes from the tubes in the form of colourless drops, the axis cylinder is dissolved, and the yellow sheaths are left empty, dilated and with swollen walls of 0·0004—0·0008‴ in thickness. In nerves treated with corrosive sublimate, according to Czermák ('Zeitsh f. wissensch. Zoologie.' 1850) the sheaths are, also, often very prettily shown. It has not yet been determined whether the finest nerve-fibres in the central organs, and in the peripheral nerves (under 0·001‴) possess a structureless sheath. Analogy with the coarser fibres is in favour of the existence of such sheaths, but on the other hand there are some facts which would seem to indicate that there are also, *sheathless* primitive nerve fibres, both of the medullated and of the non-medullated kinds. I have already (in my 'Microscopical Anatomy,' II, 1, 396) remarked, that according to my observations in the Tadpole, several dark-bordered fibres are developed in one and the same structureless sheath formed by the coalescence of cell membranes; and that a similar thing (at least from R. Wagner's figures) occurs in the electric organ of the *Torpedo;* in which cases special tunics can scarcely be supposed to exist around each separate fibre. And, quite recently, Stannius ('Gött. Nachr.,' 1850) has found, in *Petromyzon*, that the nerve fibres of the central organs possess neither membranous sheath nor pulp, and are, as it may be expressed, nothing more than free axis-fibres. When to this, it is also added, that the impossibility of demonstrating membranes, by no means certainly proves their non-existence, still, the facts stated are worthy of all consideration, and we must, in this ques-

tion, for the present, abstain from all conclusions drawn from analogy.

In order to see the *medullary sheath* or nerve-pulp in its normal condition, a nerve of an animal just killed, without any addition, must be quickly brought under the microscope; in which case some isolated fibres will always be seen quite unchanged, although, as the nerve dries, they are very rapidly altered. Besides this method, I would also recommend the examination of the nerves in the transparent parts of animals, either alive or just killed (nictitating membrane, mucous membrane of the Frog, tail of Tadpole, &c.), the observing of them on warmed pieces of glass (Stark.), and after treatment with chromic acid, which frequently preserves, particularly the cerebral fibres, quite uninjured. The nerve-pulp or medulla is obviously a viscid, fluid, extensible, glutinous substance, to be compared in point of consistence with thick oil of turpentine, and which under pressure assumes all possible figures, appearing in the form of globules, filaments, and membranous masses, of very different aspects, with pale or dark borders, and opaque or clear. In chemical composition it consists principally of fatty matter.

The central filament of the nerve-fibres, which was perhaps seen as early as by Fontana, and with which we have become better acquainted under the name of "primitive band" given to it by Remak, or "cylinder-axis" as it has been termed by Rosenthal and Purkinje, is indisputably the most difficult of investigation, and the least known portion of the nerves. There is no microscopist who has not frequently seen this axis-fibre, but it may, without fear of contradiction, also be asserted, that there is none, not even excepting Remak himself, its discoverer, who can boast that he has studied and learned its relations in every particular. For this reason, but few, as Hannover and J. Müller, are unconditionally agreed with Remak and Purkinje in regarding the axis-cylinder as a constant element in recent nerve, whilst most observers have adopted the views of Valentin ('Repert.' 1838, p. 76, 1839, p. 79), and Henle ('Allg. Anat.'), who regard it as not always present, but rather as a secondary formation, which does not exist during life, and as the uncoagulated central portion of the contents of the nerve-fibre, which, during life, are homo-

geneous. I have endeavoured to the utmost of my power to investigate the relations of this structure, and have arrived at the following results:

1. *The axis-cylinder, is constantly present in every nerve-fibre, both central and peripheral, in fine and in coarse fibres, and after death is apparent before the nerves are treated with any reagent whatsoever.* In the human nerves, in the brain and spinal cord, as they are commonly obtained for examination, the axis-cylinder, when duly sought for, is *everywhere* and with *certainty* to be recognised; and in fact by far the most easily in the central organs, where the absence of neurilemma and the delicacy of the nerve-sheaths oppose but little hindrance to the tearing asunder of the fibres. *In these situations it may be seen in nearly the finest fibres.* It always presents the aspect of a pale filament, which, together with a tolerable degree of consistence, is still very flexible and at the same time highly elastic, as may be readily observed on compression of small portions of the spinal cord (in which case very many axis-cylinders are stretched and torn, retracting considerably and forming undulating curves). On the average it is about one third as wide as its nerve-fibre, and consequently varies a good deal in diameter, is obviously quite solid, most generally homogeneous, but not unfrequently also, faintly striated or very finely granular. It most usually follows a straight course, bordered by two parallel, pale contour lines, occasionally, however, it is, in parts, thicker or more slender, though it never presents varicosities like the nerve-fibres; and it may, moreover, be curved or even slightly undulating, and also perhaps with an irregular, even jagged border.

2. *When recent nerve-fibres of an animal just killed are treated with proper reagents, the axis-fibre instantaneously appears.* If a thin cutaneous nerve of the Frog, whilst under examination with a power magnifying 100 times—be touched with a drop of *glacial* or *concentrated acetic acid,* the nerve retracts and there appear instantaneously, at each of the cut ends, large particles of the grumous nerve-pulp, and pale, clear fibres; and the same thing happens if the nerve have been previously teased out, and the fibres brought separately into view. The clear fibres are evidently the axis-fibres, as they may readily be traced into the projecting medullary sheaths and entire nerve-tubes,

and in other respects, also, present all the characters of those fibres, only that they are much paler and broader (as much as 0·004‴ in the peripheral thick fibres) and evidently swollen; they frequently, also, appear convoluted, or even spirally rolled, which is owing, simply to the shortening of the whole nerve caused by the acetic acid. The nerve-pulp itself is rendered grumous by the same reagent; the grumous particles are sometimes granules, sometimes very short rods, like fat-crystals, which latter may be very often seen on the nerve-fibres, forming stellate, acicular groups (margaric acid); alcohol and ether, also render the axis-cylinder very distinct, both, when recent nerves are treated with those reagents in the cold, in which case their action must be rather more prolonged, and when they are boiled in them. I can particularly recommend the boiling in absolute alcohol, by which means excellent preparations of the axis-fibres may be made, and in the shortest time. Under this treatment the nerves become firmer, but still admit of being readily torn into fibres, and always exhibit very numerous, isolated central fibres of considerable length, which, contrasted with those brought into view by means of acetic acid, are, as it were, contracted (at most 0·002‴ wide), yellowish, firmer, and often convoluted or twisted. Ether acts in the same manner. By both reagents the medullary sheaths are rendered paler and grumous, the grumous particles frequently appearing, as it were, to be united into a delicate network. When nerve-fibres are boiled, first in ether and afterwards in alcohol, they become quite pale, but the sheath and axis-cylinder perfectly distinct, the latter presenting precisely the same appearance as after treatment with alcohol alone. Consequently, it would seem, that the axis-fibres contain no trace of fatty matter; at all events, except that they shrink a little, they are not altered by the action of ether and alcohol, and afterwards, also, again enlarge, under acetic acid, into broad pale bands. Besides the reagents above mentioned, the axis-fibres are particularly well displayed by chromic acid (Hannover), corrosive sublimate (Purkinje, Czermàk), and gallic acid, but less readily in recent nerves, in which, it is true that they become instantaneously manifest, although it is never, except by accident, and rarely, that they can be isolated, than, especially after a more prolonged immersion in those fluids. The nerve-fibres under these

circumstances appear contracted, the medullary sheath grumous, the axis-cylinder more opaque and somewhat diminished, in chromic acid yellowish, but in other respects exactly as above described. In the acoustic nerve of the Sturgeon, Czermàk, by means of corrosive sublimate, has demonstrated, in dividing nerve-fibres, the existence, also, of bifurcating axis-cylinders. Iodine also or iodine combined with aqueous hydriodic acid (Lehmann) act very powerfully. In quite recent nerves it instantaneously renders the medullary sheath wholly grumous, and, not only isolates numerous, somewhat shrunken axis-fibres, for a considerable length, but renders them in many nerve-fibres very distinct *in situ*, and usually appearing convoluted or serpentine. Hydrochloric-, sulphuric-, and fuming nitric acids, in certain cases, also render the axis-cylinders apparent (Lehmann).

3. *The axis-cylinder consists of a solid protein compound differing from common fibrin, and from the fibrin of the muscles.* The chemical nature of the axis-cylinder is difficult of investigation, because it cannot be obtained in an isolated form in large quantity; something, nevertheless, may be learned from microchemical reaction as has been shown by Lehmann and myself. In concentrated acetic acid it swells up considerably, but is dissolved with difficulty, and even after it has been boiled continuously for several minutes, although pale, it always remains unchanged. When boiled for a longer time in acetic acid it dissolves, exactly like coagulated albumen, whilst the sheaths and some of the contents remain undissolved. Alkalies (potass, soda, ammonia), in the cold, attack the axis-cylinder but slowly, though in soda it instantaneously becomes very pale and swells up to 0·004—0·005 or even 0·006‴. Longer immersion in soda dissolves it, and the same thing takes place upon its being boiled, soon after the commencement of ebullition in the fluid. In fuming nitric acid, it disappears in a short time—less than half a minute,—exactly as is the case with coagulated albumen. Treated with nitric acid and potass the axis-cylinder is rendered yellow (xanthoproteinic acid) and may be seen spirally contracted, within the nerve-fibres, which are also shortened, but not to the same extent. On the other hand it is not coloured by sugar and concentrated sulphuric acid, which redden coagulated albumen, at most acquiring a yellowish or pale-reddish hue. In water the

axis-cylinder is unchanged, even when boiled, in which case it is readily isolated and appears somewhat contracted; by ether and alcohol it is undissolved even by boiling, but shrinks to some extent. The latter effect is produced also by corrosive sublimate, chromic acid, iodine, and carbonate of potass. Viewing all these reactions together, it might perhaps be stated with certainty, that the axis cylinder is a coagulated protein compound which, however, differs from fibrin, inasmuch as it is insoluble in carbonate of potass and solution of nitre, and offers much greater resistance to acetic acid and caustic alkalies. On the other hand, it agrees with the substance of which the muscular fibres are composed, in its elasticity and insolubility in carbonate of potass, differing from it in its insolubility in dilute hydrochloric acid, and difficult solubility in acetic acid.

These are the most important facts connected with the axis-cylinder. The conclusion which may be drawn from them, appears to me, to be simply this, that the axis-cylinder is not an artificial product, but that it must be regarded as an essential constituent of the living nerves. The only objection which can be urged against this opinion consists in the circumstance, that the axis-fibre cannot be seen in living fresh nerves, and that it cannot generally be distinguished, as a special structure, in the interior of the nerve-tubes without the aid of reagents. But it must be remarked that it *can also be brought into view in nerves that are still warm.* Thus I find well-marked projecting axis-fibres at the roots of the cerebral nerves in Frogs just killed, which I have examined as quickly as possible, after the application of a solution of sugar, particularly in those of the optic, trigeminal, and *vagus,* also in the spinal nerves, for instance in the second. I see them under the same conditions in the peripheral nerves of the Frog that have been teased out, and, in these nerves, have on several occasions, even distinctly noticed the axis-fibres in the form of convoluted filaments, in larger drops of the nerve-pulp expressed from the tubes (fig. 137, 2). The only fact, therefore, that can be adduced in opposition, is this, that it is quite true that the axis-fibre cannot, with certainty, be perceived *in the interior* of the recent nerve-tubes themselves, except upon the application of some reagent; but this circumstance obviously proves nothing at all, because neither can it be seen in the interior

of tubes of less recent nerve substance, all of which, as innumerable examples of isolated axis-fibres occurring in them, show, invariably contain such fibres. The axis-cylinder, possessing the same refractive power as the still fluid part of the medullary sheath, is necessarily indistinguishable from it, but from this circumstance we cannot conclude that it is absent, nor, equally, can such a conclusion be drawn from its invisibility in the recent nerve-fibril. Taking all these circumstances together, I am firmly convinced that a special, central structure exists even in recent nerves, which is distinguished from the more external portion,—that is, from the medullary sheath,—not only by its chemical composition, as appears to me to have been placed beyond all doubt, but also by its consistence and elasticity, as well as by its possessing a determinate form. The condition in which we obtain the axis-fibre in the human nerves and central organs, by the addition of the serum of the blood, albumen, or vitreous humour, appears to me to represent its natural state; on the other hand alcohol, ether, iodine, corrosive sublimate, gallic-, and chromic acid render it more consistent than it is normally; whilst acetic acid, dilute nitric acid, and alkalies exhibit it paler and more swollen. The nerve-pulp forms a semi-fluid cortex around the axis-fibre, and, though intimately connected, is not continuous with it. By pressure, therefore, the pulp may very frequently be expressed, by itself, from the ends of the tubes or from lateral rents of the sheath. The drops of pulp thus formed, usually coagulate on the surface, remaining clear and transparent in the interior, like the central portion of the nerve-tubes. Many authors have described these bodies as portions of the whole contents of the nerve-tube, and have regarded their formation as a proof against the pre-existence of the axis-fibre, but incorrectly. They belong to the medullary sheath only, which, in the interior of all nerve-fibres with only a double contour, is still for some space perfectly clear and bright. An *axis-fibre and a clear space, in fibres having a double contour, are therefore by no means identical,* and it is not at all surprising, nor opposed to the existence of an axis-cylinder, that a multitude of drops with a double contour and clear contents should be obtained from such fibres. The medullary sheath may also coagulate entirely, and then the axis-fibre remains evident,

sometimes as a transparent streak of uniform breadth throughout; sometimes, when the grumous particles are more numerous, it may be concealed by them, so that the entire contents of the nerve appear to be coagulated. They are so, however, only in appearance, the clear fibre always lying in the interior; and I have never yet seen it coagulated or grumous. Non-medullated nerve-fibres occur in many situations. I enumerate among them: 1. the pale fibres in the Pacinian bodies; 2. the nucleated pale fibres in the terminations of the olfactory nerves; 3. the perfectly transparent, non-nucleated nerve-fibres in the *cornea;* 4. the pale, branched, and partially anastomosing terminations of the nerves in the electrical organ of the Torpedo and Ray (R. Wagner, Ecker); 5. the similarly constituted terminations of the nerves in the skin of the Mouse (*vid.* 'Mikroskop. Anatomie,' § 11); 6. the pale processes of the nerve-cells in the central organs and ganglia, even though they may not all pass into dark-bordered fibres. Of these fibres, those which occur at the extremities of nerves were, even by the earliest observers of them, unconditionally regarded as nerve-fibres; and as respects the processes of the nerve-cells, I described this to be their nature as early as the year 1846; but these views could not be considered as fully established, until the relation of the fibres with the elements presenting the dark borders was completely elucidated. But since it has been ascertained by Schwann, Ecker, and myself, that the nerve-fibres of the embryo are in precisely the same condition as the pale fibres now in question, and since I, Wagner, Robin, and Bidder and Reichert, have shown that the pale processes of the nerve-cells pass into dark-bordered fibres, it has become more possible to arrive at positive conclusions on the subject. R. Wagner was the first to broach the supposition, that the pale fibres in the Pacinian bodies, and in the electric organs, were nerve-sheaths, with axis-cylinders, and that the processes which pass into nerve-fibres, were themselves bare axis-cylinders, and, moreover, that the entire granular contents of a nerve-cell are nothing but an axis-cylinder enlarged into a globular form; and after I had demonstrated the constant existence of the axis-cylinder in the living nerve, and that it was a structure distinct from the medullary sheath, I considered myself fully justified in asserting *that the dark-bordered nerve-fibres were in direct connection on*

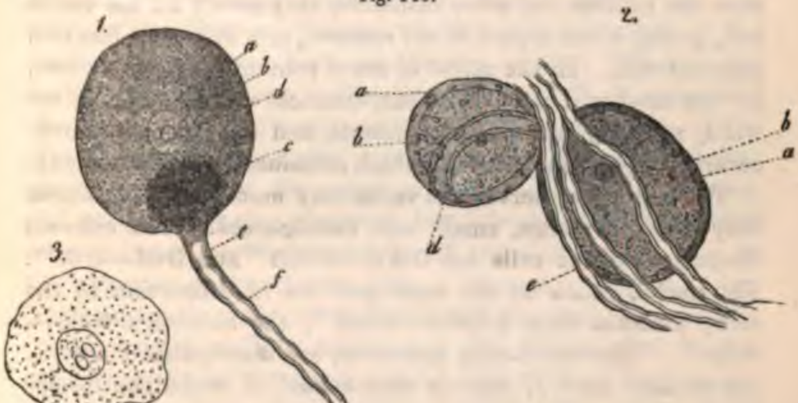
the one side through the axis-cylinder, with the pale processes of the nerve-cells and the contents of those cells, and on the other, that they passed into the pale terminal nerves in the situations above mentioned. But this, by itself, as I believe, affords no ground for the identification of the pale fibres in question, or the contents of the nerve-cells, with the axis-cylinders. This could only be established, if we knew with certainty that the medullary sheath of the dark-bordered nerve-fibres is superadded from without to the contents of the pale embryonic fibres during the development of the nerves, and is an entirely new formation between those contents and the membranous sheath. This is not the case, however, it being on the contrary more probable that the medullary sheath, which is also albuminous, is developed merely from a metamorphosis of the outermost part of the embryonic nerve-contents, that is to say from the development of fat in it, and that the axis-cylinder is the unaltered innermost part of those contents. In this case all the structures, the nature of which we are now discussing, would represent, not bare axis-cylinders, but an entire embryonic nerve-tube, the contents of which were still homogeneous, or had not undergone differentiation, and would also be in continuous connection with all the parts of the dark-bordered fibres,—a mode of explaining them to which, at all events at present, I am disposed to give the preference. In addition I would remark, that the *pale nerve-fibres are also met with in different stages of development.* The nucleated fibres in the olfactory membrane remain altogether in the stage of embryonic fibres, as also, to all appearance, do the pale ramifications in the electric organ, and the contents of both these kinds of nerve-tubes would appear to have little agreement, in their consistence, with an axis-fibre; in the Pacinian bodies the contents of the pale fibres, in all respects, represent an axis-fibre, for it is probable that a sheath also exists in this situation; in the cornea, the contents of the transparent terminal nerve-tubules are apparently more fluid; and, lastly, with respect to the processes of the nerve-cells, they consist, whether they have a delicate sheath or not, of a substance often exactly resembling an axis-cylinder, but which is also frequently of softer consistence, corresponding with the contents of the nerve-cell. The contents of the pale non-medullated nerve-tubes, therefore, although genetically

comprehending more than an axis-fibre, still in all probability are capable pretty nearly of assuming its nature.]

§ 111.

The *nerve-cells*, (accessory corpuscles (Belegungskörper), nerve-corpuscles, Valentin), (fig. 140), are nucleated cells, occurring in great numbers in the grey or coloured substance of the central organs, in the ganglia, and occasionally also in the trunks, and peripheral expansions of the nerves (*retina*, *cochlea*, vestibule). The nerve-cells are covered externally by a delicate, structureless *membrane*, which in the cells of the ganglia (ganglion-cells, -globules, -corpuscles), may be demonstrated easily, but with great difficulty in those of the

Fig. 140.



central organs; the application of re-agents, however, will suffice to show, pretty distinctly, that the membrane exists around the larger cells, even in these situations, whilst in the smallest, just as in the finest nerve-fibres, no membrane has

Fig. 140. Nerve-cells, × 350 diam., from the acoustic nerve: 1, nerve-cells with the origin of a fibre, from the anastomosis between the facial and auditory nerves, in the *meatus audit. int.* of the Ox; *a*, membrane of the cell; *b*, contents; *c*, pigment; *d*, nucleus; *e*, continuation of the sheath upon the nerve-fibre; *f*, nerve-fibre: 2, two nerve-cells with fibres, from the *n. ampull. infer.* of the Ox; *a*, sheath with nuclei; *b*, membrane of the cell; *c*, nucleus; *d*, the origin of a fibre with nucleated sheath: 3, isolated contents of a nerve-cell, with nucleus and two nucleoli. For these drawings I am indebted to Dr. Corti.

yet been observed, although one probably exists. The contents of the nerve-cells are a soft, but tenacious, elastic substance, which besides the nucleus consists of two elements; firstly, of a clear, homogeneous, light-yellowish, or colourless *matrix*, upon which the physical properties of the contents depend, and which is a protein-compound; and, secondly, of minute granules of different kinds. In the colourless nerve-cells these present the form of uniform, roundish, for the most part, minute and pale, more rarely, darker and larger corpuscles dispersed throughout the entire contents of the cell, and imbedded in the tenacious matrix; whilst in the coloured cells, instead of these granules, more or less yellowish, brown or blackish corpuscles occur. The latter are most usually of a larger size, and are placed, closely aggregated, in a mass near the nucleus; in other instances, they nearly fill the entire cell, giving it the aspect, in all respects, of a brown or blackish pigment-cell. In the midst of these contents lies the *nucleus*, for the most part as a very clear, spherical vesicle with distinct walls, perfectly transparent contents, and one, or more rarely several, large opaque nucleoli, which occasionally exhibit a cavity.

The size of the nerve-cells varies very much; like the fibres, they occur as large, small, and middle-sized. The extreme dimensions of the cells are 0·002—0·003‴ and 0·05—0·06‴. The nuclei, which for the most part are in proportion to the cells, measure from 0·0015—0·008‴; the nucleoli 0·0005—0·003‴. The nerve-cells, moreover, are distinguished according as they are: 1. *thin* or *thick-walled*, of which the former are found almost wholly in the spinal-cord and brain; and 2. as they are *independent cells*, or are *furnished with pale processes*, of which they may have one, two, or several (uni-, bi-, multipolar cells), and which are frequently ramified, and the former, in many situations, continuous with dark-bordered nerve-fibres, and even having the nature of non-medullated nerve-fibres. Besides the nerve-cells, there also exist in the grey substance of the higher central organs, as constant constituents, a *finely granular pale substance*, which has the greatest resemblance to the contents of the cells, and besides this, in places, large accumulations of *free cell-nuclei*. Similar elements are contained in the *retina*, and according to Wagner and Robin in the ganglia of the Plagiostomata.

[The nerve-cells are simple cells, as which they were understood even by Schwann; this is clearly and manifestly shown by their form, their chemical composition, and their development. When Bidder, more lately (l. c.), relying upon the fact that the nerve-cells in many situations are in connection at each end with dark-bordered nerve-fibres, propounds the opinion that they are membraneless masses, imbedded in dilatations of the nerve-tubes, he has overlooked those cells from which no fibres are given off, which possess exactly the same membrane as those with processes; and has not considered that there also exist nerve-cells with a single, and others with numerous processes, as applied to which, his view would be altogether unnatural; and lastly, that the development of these bodies indicates that the nerve-cell is formed, *in toto*, whether it possess processes or not, from a simple cell. It has not yet been determined whether the nerve-cells of the large central organs have membranes or not; Stannius was unable to detect them in the Lamprey, and R. Wagner says the same of the nerve-corpuscles of the electric lobes of the Ray. I think I have seen a membrane in the large, many-rayed corpuscles in the spinal-cord and cerebellum of man, and occasionally, also, in others, but I freely acknowledge that no membrane can be detected in all the smaller cells, nor in the processes of the central cells in general. This does not, however, appear sufficient to justify the denial of the existence of membranes in these instances, and I believe, that in this case, as in that of the finest nerve-tubes, we must for the present abstain from any definitive opinion. The processes of the nerve-cells, in the brain and spinal-cord, which were first noticed by Purkinje, will be more minutely described when we come to speak of the central organs, and the question will there be discussed as to their relation to the central fibres. In the ganglia, there are no cells with branched processes, instead of which we find only those with one, two, rarely three or four, pale appendages, which are continuous with dark-bordered tubes. The nerve-cells consist, for the most part, of a coagulated, although soft protein-compound, which appears to correspond very closely with that of the axis-fibres. It has not been ascertained whether the membranes and nuclei differ essentially from it. The fatty matter, which has also been

found in small quantity in the grey substance, constitutes in every case the opaque granules in the cells, and appears to exist in other conditions also, in their contents. When isolated nerve-cells are compressed, they become much flattened, resuming their pristine form when the pressure is removed. Their processes also are very elastic, and like the axis-fibres may be considerably extended, and afterwards again retract themselves.

As our knowledge of the *chemical composition* of the grey and white substance still leaves much to be desired, I content myself with the following statements. Lassaigne, in the brain of a lunatic, found—

	Grey substance.	*White substance.*
Water	85.2	73·0
Albuminous matter	7·5	9·9
Colourless fat	1·0	13·9
Red fat	3·7	0·9
Osmazome, lactates	1·4	1·0
Phosphates	1·2	1·3

According to Frémy (Comptes rendus, tom. ix, p. 703, 'Ann. d. Chem. und Pharm. 1841,' vol. xl, p. 69), the brain (both substances together) contains—

Water	80
Albumen	7
Fatty matter	5
Osmazome and salts	8
	100

Which almost exactly agrees with Vauquelin's analysis, who moreover estimates the osmazome at 1·12, and the salts at 6·65; whilst it differs from that of Denis, who found much more fatty matter (12·40 in man 20 years old, 13·3 in one aged 78), and less water (78 and 76%).

CENTRAL NERVOUS SYSTEM.

§ 112.

Spinal Cord.—The nervous elements are so disposed in the spinal cord, that its external, white substance is constituted almost exclusively of nerve-fibres, whilst the grey nuclear por-

tion with its prolongations, the *cornua*, or horns, is formed, in almost equal proportions, of nerve-fibres and cells.

The *white substance* of the spinal cord may, for the purpose of description, be most conveniently, and in accordance with usage, divided into two halves, and each of these into three columns. The anterior columns (*funiculi anteriores*), are, towards the interior, almost completely separated from each other by the anterior fissure (*fissura anterior*), which extends the whole length of the cord, and into which a vascular process of the *pia mater* penetrates. At the bottom of the fissure, however, the columns are united by the *anterior*, or *white commissure* (*com. alba*); externally, they extend as far as the points of exit of the anterior roots of the nerves, or to the *sulcus lateralis anterior*, but are here inseparably connected with the lateral columns (*funiculi laterales*), which again, at the points of exit of the posterior roots, where the *sulcus lateralis posterior* is situate, are continuous, without any line of demarcation, with the posterior columns. The latter (*funiculi posteriores*) appear indeed as if they were in contact in the posterior mesial line, because the posterior longitudinal fissure described by many anatomists, does not exist in man, except in the lumbar enlargement of the cord, and in the superior cervical region; but they are nevertheless separated, to such a degree, throughout the whole length of the cord by very numerous vessels, which in the posterior mesial line penetrate as far as the grey nuclear portion, that the columns in most places are not even in contact, and even where they are, they are merely in juxtaposition, and never by any means continuous into each other. Thus the white substance of the cord represents two halves, united only by the anterior white commissure, and each of which is divided more artificially into three columns, which occupy the depressions left between the projecting processes of the grey substance.

The *grey substance* presents a central portion, more of a riband-like form, and four laminæ projecting laterally from it, so that its transverse section forms a cross. The *central portion* or the *grey commissure*, in the adult, does not, normally, contain any canal, such as exists in the fœtus, and consists of a central, cylindrical, or flattened tract, constituted principally of nerve-cells, of a yellowish colour,—the *grey nucleus*

(*subst. grisea centralis*), and of nerve-fibres running transversely, continued beyond the nucleus, before and behind it—the *grey*, or *posterior commissures*. Of the laminæ, in a transverse section also termed *horns*, the anterior are thicker, and shorter, of a uniform grey colour, composed of larger and smaller nerve-cells, and of delicate nerve-fibres of medium fineness; the posterior, longer and thinner, are constituted at their roots like the former, only most usually of smaller cells; but at the free edge are invested with a more transparent layer, containing a preponderance of smaller nerve-cells—the *substantia gelatinosa* of Rolando. Of the roots of the spinal-nerves, the anterior penetrate between the anterior and lateral columns, directly to the anterior horns, and the posterior are lost between the lateral and posterior columns, passing through the *substantia gelatinosa* into the posterior laminæ or horns.

Fig. 141.

With respect to the intimate structure of the spinal-cord, we have to distinguish, in the *white substance*:—1. horizontal; and 2. longitudinal *fibres*. The latter, in all situations, except in the anterior commissure, are in great part altogether unmixed with horizontal fibres, and everywhere, both superficially and deeply, run parallel with each other, but they are never interlaced, nor do they ever constitute smaller fasciculi. The number diminishes from above downwards, because, as

Fig. 141. Transverse section through the spinal cord in the superior lumbar region, magnified about 30 diam., half diagrammatic: *a*, anterior column; *b*, lateral columns, motor portion; *c*, lateral columns, sensitive portion; *d*, posterior columns; *e*, anterior longitudinal fissure; *f*, posterior longitudinal fissure; *g*, motor roots; *h*, their internal fasciculus; *i*, their external fasciculus; *k*, decussation of the anterior columns in the anterior commissure; *l*, grey fibres of the lateral columns passing into the anterior grey commissure; *m*, grey central nucleus, here internally with two groups of somewhat darker cells; *n*, posterior grey commissure, with a vessel cut across; *o*, fibres of the posterior column passing into the grey commissure; *p*, fibres of the sensitive roots going off to the lateral columns; *q*, similar fibres entering the posterior column; *r*, longitudinal fasciculi of fibres passing into the sensitive roots; *s*, substantia gelatinosa, with traversing bundles of the sensitive roots, *w*; *t*, sensitive radical fibres running horizontally forwards to the grey commissure; *u*, large cells of the anterior cornua (the puncta), inner group; *v*, the same, outer group.

will be afterwards shown, they successively pass inwards towards the grey substance, presenting the general characters of the central nerve-fibres; that is to say, the delicacy of sheath, disposition to the formation of varicosities, and to the breaking up into separate fragments, which are constituted either of all the elementary parts of the nerve-tubes, or consist of nothing more than an axis-fibre, or of the medullary-sheath. Their diameter amounts to 0·0012—0·0048‴, on the average 0·002—0·003‴, and, in one and the same fibre is, evidently, always nearly the same, since, in the white substance, neither divisions nor any other kind of alteration in diameter of the fibres are found to exist. The *transverse fibres* occur:—1. in those portions of the lateral and posterior columns which adjoin the horns of the grey substance, and the description of which will be given afterwards with that of the grey substance; 2. in the white commissure; and, 3. at the points of entrance of the roots of the nerves. The *white*, or anterior commissure (fig. 141, *k*) is not a commissure in the common sense of the word. It is formed by those nerve-fibres of the anterior columns, which are, in succession, the most deeply placed, and which bending obliquely inwards, cross in front of the grey commissure; the fibres coming from the *right* anterior column, passing, in a radiating manner and horizontally, to the *left* anterior horn of the grey substance, and those from the *left* anterior column passing in like manner to the *right* anterior horn. The anterior commissure, therefore, represents a *decussation*, or *crossing* of the *anterior columns*, and would be better designated as such. It varies both in thickness and breadth; it is thickest in the region of the two enlargements, and is least so in the middle of the dorsal portion of the cord. Its breadth is regulated pretty nearly by that of the cord, and of the bottom of the anterior fissure; being greatest in the cervical enlargement, and from this point decreasing pretty uniformly in both directions. The decussating fibres measure 0·0012—0·003‴, and, as they diverge in the anterior horns, evidently in some degree decrease in diameter.

The roots of the spinal-nerves (fig. 141, *g*, *w*), without any communication with the longitudinal fibres, are continued, in larger fasciculi, from the *sulcus lateralis anterior* and *posterior*, either horizontally or slightly ascending between those fibres,

in order, all of them, to enter the anterior and posterior, grey laminæ, where we shall again meet them. Their nerve-fibres (in the posterior roots, about $\frac{2}{3}$ measuring 0·004—0·008‴, and $\frac{1}{3}$ 0·0012—0·003‴, in the anterior about $\frac{3}{4}$ measuring from 0·006—0·011‴, and $\frac{1}{4}$ 0·0025—0·003‴) present, as soon as they have entered the cord, all the characters of the central fibres, the largest, at their commencement, measuring about 0·004—0·006‴ in the sensitive, up to 0·008‴ in the motor roots. They continue, however, distinctly and constantly decreasing in size, until ultimately, the former, when they enter the grey substance, have a diameter of scarcely more than 0·0012—0·0028‴, and the latter in like manner one of not more than 0·004‴ (or in some of 0·006‴).

In the *grey substance*, the nerve-cells and fibres deserve special consideration. The former present very various forms, all, however, corresponding in one respect, that they are invariably furnished with processes or prolongations, and, for the most part, with many such, which repeatedly branching, ultimately terminate in extremely fine, pale fibrils, like the finest axis-fibres. I distinguish :—1. The cells of the central grey substance. These (fig. 142) are 0·004—0·008‴ in size, always pale and finely granular, with multiple nuclei and branching pale processes, constituting as it would seem the principal bulk of the central grey substance; but in which, dark, true nerve-fibres also occur, although of nearly the finest kind, which can scarcely be recognised as such, and are indeed very few in number, and quite isolated; besides these, there are a good many extremely fine, pale fibrils, like the processes of the cells, only more extended, and running in a transverse and longitudinal direction, of which nothing more can be said, as

Fig. 142.

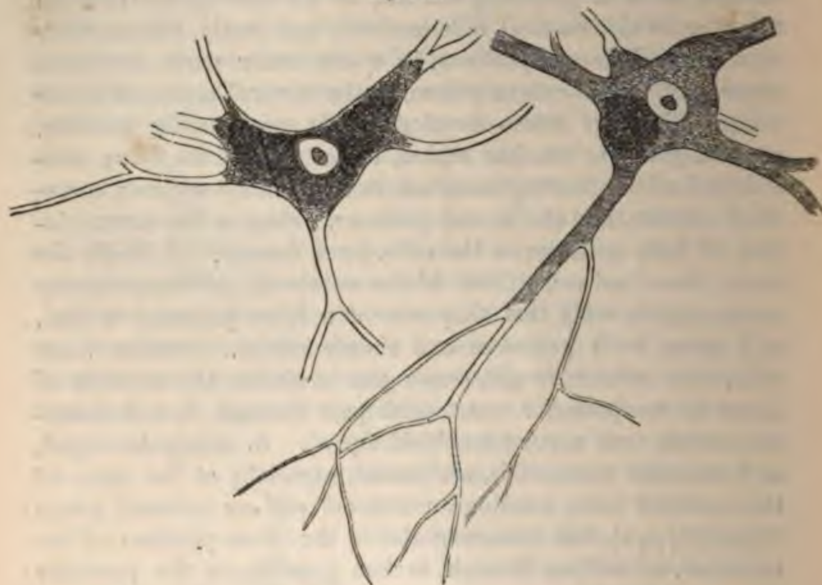
Fig. 142. Cells from the grey central nucleus of the cord in Man, × 350 diam.

to whether they are nerve-tubes, or are to be referred to the processes of the cells. The grey central substance, taken altogether, is thickest in the lumbar enlargement, and on a transverse section is of a pyriform, scutate, or cordate figure; next to this stands the cervical enlargement; and lastly, the superior cervical and dorsal portions, in which latter parts its transverse section presents an ellipse, in the cervical region, with the longer diameter much developed. It occasionally exhibits, especially in the lumbar region, indications of its being constituted of two halves, inasmuch as the middle appears somewhat clearer, and the lateral portions, owing to the accumulation of fatty granules in the cells, more opaque. 2. With the above-described cells, those of the *substantia gelatinosa* pretty nearly agree, only that they are of a faint yellowish colour, and have 1—3 processes and simple nuclei. Besides these cells, the *substantia gelatinosa* also contains the fasciculi of fibres of the posterior roots which pass through it, and numerous other true nerve-fibres (*vid. infra*). 3. Much developed, well marked nerve-cells, are seated, especially at the apex of the anterior horn, forming an internal and an external group (fig. 112, *u*, *v*), but occurring also in the other portions of the anterior, as well as, though in less number, in the posterior horns, whilst they are never met with in the *subst. gelatinosa*, nor in the grey commissure. All these cells (fig. 143) are 0·03—0·06‴, in size, with nuclei measuring 0·005—0·008‴, are fusiform or polygonal, frequently containing brown, pigmentary matter, and furnished with from 2 to 9, or even more branched processes, which at their origin are often 0·004—0·005‴ thick. These processes may be traced to a length of 0·1—0·24‴, and ultimately terminate in fine fibrils, all of which, scarcely more than 0·0004‴ thick, are contained within the grey substance. Besides these large and, for the most part, many-rayed cells, there are also found in the grey substance, though more widely scattered among its nerve-fibres, very numerous, smaller cells, which constitute a complete series between the large cells and those of the *substantia gelatinosa*, and consequently require no further description.

The nerve-fibres of the grey substance are excessively numerous, so much so as to constitute in any case the half of its bulk, if not more, and exhibit the same conditions as those of

the medullary substance, except that, on the average, they are not more than half as thick, or even less (not more than

Fig. 143.



0·0008‴); fibres, however, also occur of the same size as those in the white substance and in the entering roots of the nerves, especially in the anterior horns, though more widely scattered, and principally towards the anterior roots. The investigation of the *course* of these nerve-fibres in the grey substance is one of the most difficult tasks in microscopy. If we observe, above all, the roots of the *peripheral nerves* (figs. 141, 144), it is apparent:—1. that the motor filaments in them, after they have entered the *sulcus lateralis anterior*, and the contiguous portions of the anterior and lateral columns, and penetrated horizontally between the longitudinal fibres of the white substance, are continued further in the grey substance of the anterior horns, principally in two directions. The fibres of one bundle, and indeed of that which enters the most internally (fig. 141, *h*), proceed directly backwards and

Fig. 143. Large nerve-cells with processes from the anterior cornua of the spinal cord in Man, × 350 diam.

a little inwards, without forming any plexus, or sub-dividing to any considerable extent into subordinate fasciculi, to the innermost portions of the anterior horns, skirting the anterior columns. In this course they pass through the inner group of the many rayed, large nerve-cells, in perfectly compact bundles, however, and having no connection whatever with the processes of the cells, as may be readily perceived under a strong magnifying power, when the individual nerve-fibres may be traced quite beyond these cells. Now, if these bundles derived from the anterior roots are traced further, it will be perceived, in favorable sections, that they extend to the lateral parts of the anterior commissure, continuing to run in the anterior horns, and, that ultimately, forming more or less well-marked curves, they are continuous with its fibres, and in fact are disposed in such a way, that the root-fibres of the right side pass into the left anterior column, and those of the left side into the right. Consequently there is established in the white commissure *a connection of the longitudinal fibres of the anterior columns and of a part of the motor roots, together with a total decussation.*

A large number of the fibres of the motor roots take no part in the above-described decussation, and are wholly unconnected with the anterior fasciculi,—these are the root-fibres which enter the anterior horns the most externally. Forming, for the most part, smaller fasciculi, or even as separate fibres, and therefore less easily observable, they run in part directly backwards, and in part arch outwards, but ultimately bend towards the anterior half of the lateral column, where they pass between the outer groups of the large, many-rayed cells of the anterior horns, and then enter the lateral column in a horizontal direction. These transverse fibres now penetrate to various depths (nearly half, or even more) into the lateral column, then curve *upwards*, and after running thus a short distance, appear as longitudinal fibres. Consequently, to express the same thing in other words, *a second portion of the motor roots arises from the anterior half of the lateral column of the same side, and quits the spinal cord without previously undergoing any decussation.*

It is, moreover, worthy of remark, that most of the fibres, perhaps all, which join the motor roots from the anterior and

lateral columns, undergo considerable changes in their diameter. Those of the anterior columns measure, as has been observed before, at their commencement, on the average, 0·002—0·004‴, in the anterior commissure scarcely more than 0·003‴, and in the grey substance hardly more than 0·002‴; and the same is the case also with those of the lateral columns; which, however, even while still in the interior of the column, where their direction is horizontal, measure scarcely more than 0·002‴. This diminution in size, however, is again succeeded by an increase in thickness, which takes place, in part, within the grey substance, in part at the point where the radical bundles quit it, the amount of which increase has been already stated in numbers; so that, proceeding from the peripheral nerves, we find them gradually diminishing in size from their entrance into the cord until they reach the grey substance, and again enlarging from the point where they join the longitudinal elements of the white substance, but not to such an extent as ever to attain, nearly their pristine diameter. Of divisions in the fibres of the anterior roots in the anterior horns, I have seen as little indication, as elsewhere in the spinal cord.

Fig. 144.

The *posterior roots of the nerves*, as has been already noticed, penetrate, like the anterior, also horizontally, or in a slightly ascending direction, from the *sulcus lateralis posterior*, through the longitudinal fibres of the white substance as far as the posterior horns.

Fig. 144. Vertical section through the cord, midway between the grey cornua and the point of entrance of the roots of the nerves, × about 25 diam.: *a*, posterior column with the sensitive roots, *h*, traversing it; *b*, *substantia gelatinosa; c*, prolongations of the posterior roots, which bend round in front of the *substantia gelatinosa* and run longitudinally, in order there to join more particularly the posterior column; *d*, basis of the posterior cornua, with the ends of the horizontal portion of the sensitive roots apparent (owing to their being cut across); *e*, anterior cornu with the large nerve-cells (the spots), and the also horizontal and divided continuations of the motor roots; *f*, anterior column traversed by the motor roots, *i*.

Here they divide into separate, slenderer, or thicker fasciculi (from 0·01—0·02‴) (figs. 141, *s*, 144, *b*), and continue, each bundle by itself, in a straight course, and without any direct connection with nerve-cells, quite through the *substantia gelatinosa* into the *substantia grisea*. In this course they follow two directions. One portion of them bends upwards, in a uniform curve, or nearly at a right angle, proceeds in the most posterior part of the *substantia grisea*, close in front of the *substantia gelatinosa* in a longitudinal direction, and gradually joins chiefly the posterior column, but in part also the posterior portions of the lateral column, being continued further, as its longitudinal fibres (figs. 141, *r*, 144, *g*). A second portion of the sensitive roots (figs. 141, *t*, 144), penetrates, always in a fascicular form, between the above-mentioned longitudinal bundles further forwards, losing itself in the posterior and in the lateral columns, and also entering the grey commissures. In horizontal sections, the former fibres are frequently very distinct, particularly those going off to the posterior columns (fig. 141, *p*, *q*). I have seen them most distinctly in the inferior extremity of the spinal cord, below the lumbar enlargement, where they ran towards the *conus medullaris*, close up to the grey central nucleus, and did not bend backwards until they reached the posterior columns; they were also well displayed in the lumbar enlargement, between the *substantia gelatinosa* and the posterior commissure. The horizontal radical fibres, also, which proceed to the lateral columns, are often exceedingly numerous, although much less so, apparently, than those which enter the posterior columns. The connection of the grey commissures with a portion of the sensitive radical fibres, is, as regards the posterior fibres,not difficult to be seen, these fibres, in part, at least, running backwards along the posterior columns, and being continued directly into the fasciculi of the *substantia gelatinosa*. In the anterior grey commissure, I have also noticed, though not a direct connection with the sensitive roots, still, fibres which, running horizontally in a direction towards the summits of the posterior horns, entered those processes. The commissural fibres are, besides, connected not only with the sensitive roots, but also, and indeed quite evidently, with the posterior columns, and less distinctly with the lateral; from the

anterior portions of which, adjoining the base of the posterior horns, arched fasciculi pass into the commissures and become intermixed with the other commissural fibres (fig. 141, *o* and *l*). These fibres probably pass over to the opposite side, into the commissures connected with the posterior roots; in which case, like the anterior halves of the cord, a decussation of fibres also takes place in the posterior commissure. In accordance with what has been remarked, the sensitive roots derive their fibres principally from the posterior and lateral columns (the posterior halves) on their own side, and probably also through the grey commissures from the same columns on the other side.

The fibres of the sensitive roots also decrease in size as they traverse the grey substance of the posterior horns. In the roots themselves they still measure about 0·008‴; in the *substantia gelatinosa*, never more than 0·004‴; in the *substantia grisea*, 0·001—0·003‴; in the grey commissures, not more than 0·0008—0·0012‴; in the posterior and lateral columns, again, 0·0012—0·004‴; in connection with which, however, it should be remarked, that, in this situation, the increase of size in the fibres which enter these columns horizontally, is not perceptible at their commencement, as is shown more particularly in vertical sections, made in the direction from within to without, through the posterior cornua. The variation in diameter may even be directly observed, in many fibres in this situation; as, for instance, at the entrance of the roots into the gelatinous substance.

Besides these fibres, belonging to the motory and sensitive roots, there exist, in the grey substance, a considerable number of nerve-fibres not referable to the roots, and which until more is known about them may be termed *special spinal-medullary fibres*.

The *filum terminale* contains, so far as it is hollow, as a continuation of the grey substance of the cord, a grey, soft substance, consisting chiefly of round, nucleated, pale cells, like nerve-cells, and measuring 0·005—0·006‴. Besides these there occur, in its upper part among the cells, true dark-bordered nerve-fibres, of various, and for the most part small diameter, and also numerous, fine, pale fibres, the nature of which is not clear to me; that is to say, whether they are

processes of cells or belong to the finest nerve-fibres. Remak ('Observ.,' p. 18) supposes, that in the Mammalia the true nerve-fibres of the *filum* all go off in lateral branches of it, the existence of which were detected by him.

[In the investigation of the course of the fibres in the spinal cord, chromic acid, or instead of it, chromate of potass, affords the principal aid. It is not easy to hit upon the proper proportion of acid, and so to harden the cord, previously stripped of its *dura mater*, and cut across with a sharp knife at the points selected, that very thin transverse sections may be taken from it. If the solution be too much diluted, the substance of the cord remains soft in the interior and spoils, if too concentrated it becomes fragile and friable, and larger sections of it cannot be obtained. I have unfortunately neglected to estimate precisely the proper per centage of acid or salt in the solution; and can only say this much, that one of a wine-yellow colour acted the best. Objects thus properly hardened may be cut at pleasure with a razor, or other very sharp instrument, if due care be taken, particularly in the avoiding of any sawing motion; and sections suitable even for the highest magnifying powers may be procured and examined, either with or without pressure or reagents, under various degrees of enlargement. The grey substance is scarcely altered by the chromic acid, except that its elements are more easily separated, and I have in hardly any other way seen its nerve-cells, together with their processes, and the nerve-fibres, more beautifully displayed. If it be desired to examine the former, the grey substance is broken up in water, which now no longer produces any change; or, what is best, in the solution of chromic acid itself; but if the examination of the latter be wished, it is by far the best to employ diluted caustic soda or potass, which renders all the nerve-cells pale. To those who may consider the application of these reagents as too powerful for such delicate organs as the spinal cord, I would remark: 1. that, as stated by Hannover, chromic acid alters the nerve-fibres, especially of the grey substance, so little, that most of them do not even become varicose; and 2. that soda, added to a preparation made with chromic acid, does not act upon the fibres for a long time, and only so far as

to render them more transparent and their medullary contents fluid. I have never, under any circumstances, seen more beautiful nerve-tubes of the grey substance, than in preparations made with chromic acid, and I think that of all known means this is the best for their study. In employing pressure, however, great care is requisite. I make use of a *compressorium* by Nachet, which allows extremely thin covering-glass to be employed, and consequently the highest magnifying powers; if I wish to apply more considerable pressure for the study of the coarser conditions, the common apparatus suffices, with which, however, with a shorter focal distance of the microscope, only lower powers can be employed. I have had entire transverse sections of the spinal cord before me, in which it might be said, that no part was disturbed from its relative position, and yet, which admitted of the application of a magnifying power of 350 diam. I would, moreover, remark, that the most favorable place in the cord for the first investigation, is the lumbar enlargement. In this situation the cord is not so thick, but that entire sections of it may be obtained, besides which the white substance, which is only an impediment, is thin, and the roots and commissures large and more readily traced.

Whether the nerve-fibres in the cord divide, has not yet been fully ascertained, yet I think that I saw such an appearance, on one occasion, in a dark-bordered fibre, and on another in an isolated axis-cylinder. In any case such divisions cannot be frequent, otherwise I must have noticed them more often, having examined innumerable nerve-fibres and axis-cylinders, expressly with reference to this point. Anastomoses between the processes of branched nerve-fibres, which Schröder van der Kolk thinks he has seen, I must, from my experience so far, doubt, but I am not able to deny their possible occurrence.]

§ 113.

Probable course of the Fibres in the Cord.—We have found that the motor and sensitive roots do not terminate at the point where they are implanted into the grey substance of the cord, as at first sight appears to be the case, but that the greater proportion of them are curved upwards, accompanying the longitudinal fibres of the white substance. The

important question now arises, viz.: to ascertain what becomes of these fibres, whether, after running a shorter or longer distance, they terminate in the cord, or whether they all ascend to the brain. It is well known, that until recently, most observers have been of the latter opinion, which was founded less upon direct observation than on the ground of probability, until Volkmann, in his deservedly celebrated article, 'Physiology of the Nerves,' shook it to its foundations, carrying the greater number of physiologists with him. I also was among these, until I had myself investigated the conditions, for there could be no doubt that Volkmann's theory connected, in the most harmonious way, the anatomical facts and the results of physiology as at that time exhibited. When I now, notwithstanding this, abandon Volkmann's theory of the termination of the spinal nerves in the cord, I am induced to do so by weighty reasons, and much regretting that I am unable to maintain a view, which appeared to throw so much light upon many difficult parts of the physiology of the nerves, and to be in accordance with so many other anatomical conditions (ganglia, invertebrate animals).

[Volkmann, in his hypothesis of the origination of the fibres in the cord, relies upon the circumstance (l. c., p. 482, *et seq.*), that the spinal cord is not of a pyramidal form with the base above, as must have been the case had all the fibres of the roots of the nerves ascended towards the cerebrum, but that it rather presents a local increase of the nervous substance at the points of origin of large nerves, which enlargement is not confined to the grey substance, but equally involves the white. That this is the case Volkmann shows from four transverse sections of the spinal cord of the Horse, and from a comparison of the diameter of the cervical cord of *Crotalus horridus*, with that of all the nerve-roots of the same animal, which was found to be eleven times greater than the former. He also supports his view by the consideration: 1. that the enlargements of the cord are always regulated by the size of the nerves of the extremities, being sometimes wanting and sometimes enormously developed; 2. that the cord, at the points of exit of the largest nerves, instead of becoming suddenly thinner, is in most cases enlarged; and 3. that the origin of

the spinal accessory nerve in this case loses all that is remarkable in it. Now, if the spinal cord in man be examined with reference to the above points, it will present, in almost all of them, exactly the contrary of what Volkmann noticed in animals. In the first place, *the white substance constantly increases in thickness from below upwards, and the enlargements of the cord depend upon an increase of the grey substance more than anything else.* That this is the case, is evident at a glance, when sections, such as are represented, after nature, in fig. 145, are compared with each other, and it also admits of being estimated in numbers (*vid.* 'Mikroskop. Anatomie,' II, 1, p. 431).

Fig. 145.

This fact being established, it remains to determine the proportion borne by the white substance in the superior cervical region to the peripheral nerves. For this purpose I instituted Volkmann's measurements in man, and in a male and female body estimated all the roots of the spinal nerves on the left side; I determined, from the ascertained diameters, the transverse sectional surfaces of all the nerves in square lines, and compared with them the transverse sectional area taken with the utmost possible nicety, of the white substance of the spinal cord, at the level of the second cervical vertebra.

It is quite true that there was now evident a very considerable difference against the spinal cord; but when the very great *attenuation of the nerve-fibres of the roots, at their entrance and in their further course in the cord,* was brought into account, which was not done by Volkmann, the matter was entirely altered, and it became clear that the cord in the male subject contained more than sufficient fibres to furnish

Fig. 145. Five transverse sections through a human spinal cord, hardened by chromic acid, to show the relative proportions of the grey and white substances,—of the natural size: *A*, from the *conus medullaris*, the diameter of the cord being $3\frac{2}{3}'''$; *B*, from the lumbar enlargement, transverse diameter $4\frac{3}{4}'''$, antero-posterior $4\frac{1}{2}'''$; *C*, from the dorsal part of the cord, $4\frac{1}{2}'''$ and $3\frac{3}{4}'''$; *D*, from the cervical enlargement, $6\frac{2}{3}'''$ and $4\frac{1}{2}'''$; *E*, from the superior cervical portion, level with the second nerve, $6\frac{1}{3}'''$ and $4\frac{3}{4}'''$.

the peripheral ones, and in the female nearly sufficient, particularly when it is considered, moreover, that in the entire enumeration, the numbers were stated rather in favour of the roots of the nerves (*vid.* the calculation in 'Mikroskop. Anatom.,' II, 1, § 116).

It appears, therefore, scarcely to admit of doubt, that the notion of a termination of the peripheral nerves in the cord, has no support in measurements such as those which, following Volkmann, I have adduced; and that the latter, even when all due allowance is made for the uncertainty always incidental to such an inquiry, *on the contrary indicate, at all events the probability, that the spinal nerves ascend to the cerebrum.* They give no further information, however, and it depends upon other facts, whether such a central origin should be admitted or not, because it is even conceivable, that the peripheral nerves may end in the cord, and that the longitudinal fibres in the cord have a wholly different source. Since it is scarcely probable that the tracing of the nerve-fibres through the entire cord will be effected either at present or perhaps at any time, it is necessary to look round for other facts, which may possibly afford conclusive evidence on the subject; and such facts do exist. In the first place, let us consider the course of the roots of the nerves in the cord, such as it has been described above. We found, that after they had all come, more or less, into contact with the grey substance, the greater number of them could be directly traced into connection with the longitudinal fibres of the anterior, lateral, and posterior columns. From this fact, together with my measurements, the passage of the greater part of the peripheral nerve-fibres into the cerebrum, will appear to many to be proved; but, not to overlook anything, it may further be remarked, that the radical fibres, running longitudinally in the substance of the cord, may terminate in it, or after running in it may again enter the grey substance higher up. The former supposition is now, it must be confessed, but little probable, because in the first place, no one has yet seen the terminations of nerve-fibres in the white substance; and in the second, because anything of the sort, for other reasons, would be very surprising, nerve-fibres being nowhere known to commence in the white substance; and with respect to the latter, any re-

entry of the roots of the nerves into the grey substance could not escape notice. Since the junction of the radical fibres with the anterior, posterior, and lateral columns, can be so well and so directly observed, the relation in question would necessarily be evident also; and yet in the course of my perfectly unprejudiced observations, I have never seen anything of the kind. Nothing, therefore, remains but to assume, that the great majority of the peripheral nerves really have a cerebral origin. Whether they all originate in the brain (where, we shall afterwards see) or in part, though, from my observations, but to a small extent, from the cord, cannot be determined, any more than the question can be decided, whether the white substance of the cord, besides the fibres derived from the peripheral nerves, also contains others passing from the brain to the cord.]

§ 114.

The *medulla oblongata* and *pons Varolii* belong to the most complex parts of the central nervous system, containing white and grey substance, intermixed in very various modes. The *white substance* is, in part, a continuation of that of the cord, in part distinct from it, and is disposed in the following manner: the anterior columns of the spinal cord diverge from each other at the commencement of the *medulla oblongata*, allowing the decussating fibres of the *corpora pyramidalia* to appear. As they proceed, a smaller division joins the *pyramids*, forming their outer part, whilst the principal portion surrounding the *olivary bodies*, internally and externally, whence they are also termed the *olivary columns*, passes laterally, and then, divided into two bundles, proceeds above the second transverse layer of fibres, through the *pons*. One of these divisions constitutes the *fillet*, (*laqueus*,) which continued above the *crura cerebelli ad cerebrum*, enters the posterior *corpora quadrigemina*, joining, within them, the corresponding division of the opposite side. The second division, or bundle, lies externally and inferiorly to the *crura cerebelli*, and enters the *tegmentum* of the cerebral peduncle. Besides this, the olivary columns, corresponding to the anterior columns of the cord, also, as it seems, give off fibres to the *pedunculus cerebelli*. The lateral columns of the spinal cord divide, on reaching the *medulla oblongata*, into three

bundles; one of which, ascending in a tolerably straight direction, is continuous with the *fasciculus lateralis* of the restiform body, and with it enters for the most part into the peduncle of the cerebellum, and in small part into the *tegmentum;* a second division penetrates forwards between the divergent anterior columns, decussates in two or three fasciculi with that of the other side (*decussatio pyramidum*), constituting the principal bulk of the *pyramids;* a third division, lastly, appears between the posterior columns at the bottom of the rhomboid fossa, or fourth ventricle, as the *eminentia teres.* These latter are continued, on the floor of the fourth ventricle and applied to each other, into the *tegmentum* of the cerebral peduncles, whilst the pyramids, passing between the first and second transverse layers of fibres of the *pons,* are continued into the base of the cerebral peduncles. The *posterior columns* of the *cord,* lastly, chiefly constitute the *fasciculi graciles* and *cuneati,* the latter of which, in great part, enter the *pedunculi cerebelli,* whilst the remainder, and the *fasciculi graciles,* situated externally to the *eminentiæ teretes,* may be traced into the tegmentum of the *crura cerebri.* All these fasciculi consist, besides the grey substance, of parallel nerve-fibres of the same dimensions as those of the cord, that is to say, from 0·001—0·004‴, seldom more.

Besides this white substance, the *pons Varolii* and *medulla oblongata,* omitting the roots of the nerves, present a system of *mostly horizontal fibres.* This system consists: 1. of the well-known transverse, arcuate fibres, external to the *corpora pyramidalia* and *olivaria;* 2. of straight fibres, which extend from before backwards, in the middle, through the *medulla oblongata,* contributing to the formation of the so-termed *raphe* (Stilling); 3. and lastly, of very numerous fibres proceeding from this *raphe* into the lateral halves of the *medulla,* following a more or less curved direction. These latter, *the internal transverse fibres,* commence behind the pyramids, and the anterior of them as a large mass, very minutely broken up by fine flattened fasciculi of the pyramidal and olivary columns, penetrate from within into the *corpus dentatum olivæ,* the white substance of which is constituted by them; they then expand in a brush-like form, and are continued through the grey substance of the *corpus dentatum,* ultimately turning

backwards towards the *fasciculus cuneatus* and *lateralis*. In this course, the fibres describe larger or smaller curves.

Fig. 146.

The latter is the case with those which come out from the posterior part of the olivary nucleus [*corpus dentatum*], and which go almost directly backwards and outwards through the *accessory olivary nucleus* (Stilling), and the grey substance, containing large cells, situated on its exterior; the former con-

Fig. 146. Transverse section through the *medulla oblongata* in Man, × 15 diam.: *P*, pyramids; *O*, olivary bodies; *F.l*, fasciculus lateralis; *F.c*, *fasciculi cuneati*; *F.g*, *fasc. graciles*; *H*, root of hypoglossal nerve; *V*, root of *n. vagus*; *F.a*, *fissura anterior*; *F.p*, *fissura posterior* in the floor of the fourth ventricle, or rhomboid fossa; *R*, *raphe*: *a*, longitudinal fibres of the *raphe*; *b*, central grey layer with transverse fibres; *c*, expansion of these fibres in the olivary column and body; *d*, accessory olivary nucleus; *e*, *hypoglossal nucleus*; *f*, decussation of the hypoglossal nerve; *g*, nucleus of the *vagus*; *hhh*, larger nerve-cells in the restiform bodies; *i*, medullary mass in the interior of the olivary body, belonging to the internal transverse fibres; *k*, arcuate fibres external to the olivary body; *l*, transverse fibres external to the pyramids; *m*, *n*, *o*, grey nuclei in the pyramids and olivary columns.

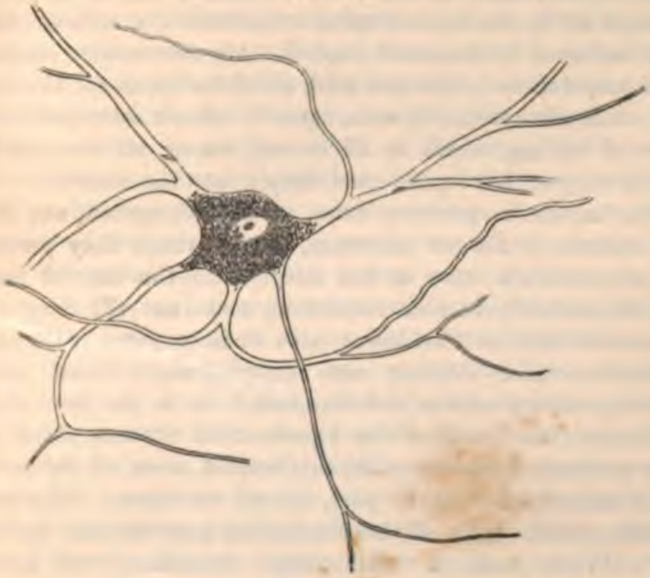
dition obtains in the anterior fibres, which spread out in a radiating manner, passing at first forwards between the pyramids and olivary nucleus, and afterwards backwards in a sharp curve, superficially round the latter, into the lateral fasciculi. A second division of the internal transverse fibres goes behind the olivary nucleus with which it has no connection, directly from the raphe, through the posterior part of the olivary columns and the *eminentiæ teretes,* outwards and backwards, also into the restiform body. All these fibres, and most of them obviously so, are associated together, and appear to me to be continued from the restiform bodies and the peduncles of the cerebellum, into the anterior divisions of the *medulla oblongata.* With respect, however, to their more intimate relations, concerning which Stilling's work and my 'Microscopical Anatomy' may be consulted, little is as yet known.

The *grey substance,* in the *medulla oblongata,* is collected into larger masses, chiefly in three situations, viz. in the olivary and restiform bodies, and on the floor of the rhomboid fossa (fourth ventricle): 1. the *grey substance* of the *olivary bodies* forms, as is well known, a folded lamella, constituting a capsule closed on all sides except the inner, which, although it occupies the situation of the anterior horns of the spinal cord, which are continued nearly to its inferior border, still has no direct connection with them; appearing, also, to be otherwise isolated from all other grey substance. Within it, besides the very numerous nerve-fibres of the transverse fibre-system, which traverse it for the most part in straight lines, there occur in great numbers smaller nerve-cells, measuring 0·008—0·012‴ in diameter, and of a rounded form, with 3—5 branching processes, and containing in the interior yellowish granules, to which the colour of the olivary bodies is due. The closest observation has failed to afford me any indication of a connection between these cells and the fibres which run among them. On a level with the two upper thirds of the olivary body, is placed, behind the nucleus and wholly isolated from it, the body termed by Stilling the *accessory olivary nucleus,* in the form of a flattened, yellowish band, of exactly the same structure as the grey substance of the olivary body, and also traversed by horizontal nerve-fibres, and in fact by fibres which have for the most part already passed through

the olivary body; 2. in the *restiform bodies*, the grey substance (*corpus s. nucleus cinereus*) assumes the form of an ill-defined, elongated mass intermixed with very numerous nerve-fibres, and which occupies mainly the *fasciculus lateralis*, but also extends into the *fasciculi cuneatus* and *gracilis*. This structure may be described as a continuation of the posterior horns of the spinal-cord, even presenting, as Stilling correctly states, an indication of the *substantia gelatinosa* of those processes, of which it may moreover be observed, that it is very remarkably developed in the uppermost portions of the cord, as far as the commencement of the decussation of the pyramids, and has a position entirely lateral. The elements of the grey substance of the restiform bodies are, besides, numerous finer fibres, which appear to pass chiefly into the horizontal, internal fibre-system, and many, rather pale, but in part brownish nerve-cells with processes, pretty regularly disposed, and most of them of the same size as those of the olivary bodies; 3. the grey substance on the *floor of the fourth ventricle*, is the continuation of the grey nucleus of the spinal-cord, and forms a tolerably thick layer, extending from the *calamus scriptorius* as far as the *aqueductus Sylvii*. It contains throughout, numerous nerve-fibres, in part of very considerable diameter, up to 0·006‴, or even 0·008‴, in part of the finer and finest kinds, and besides these, nothing but caudate nerve-cells of all dimensions from 0·006‴, up to 0·03‴, and more. The largest of these are contained in the *ala cinerea* at the posterior extremity of the fourth ventricle, and in the *subst. ferruginea s. locus cinereus* (fig. 147), in which latter situation, the cells also present well marked pigmentary matter, and very numerous, delicately branched processes. The small multinuclear cells, which in the grey nucleus of the cord occur in the form of a compact structure, are here entirely wanting, not being found beyond the *decussatio pyramidum*. Besides these three masses of grey substance, which can in part be referred to that of the spinal cord, there are found, in the *medulla oblongata*, some small collections of it, as in the pyramids near the olivary bodies, and in the olivary columns, external to the accessory nucleus, in all of which, as has been already stated by Stilling, are also to be seen in part larger cells, all caudate (in the latter situation measuring as much

as 0·025'''), and finer nerve-tubes. One part of the grey substance just described, that namely of the anterior half of the

Fig. 147.



fourth ventricle, belongs properly to the *pons Varolii.* It also contains, in its interior, besides the just described elements, above the transverse fibre-layer, both in the middle as well as more laterally, many accumulations of grey substance, with larger and smaller (as much as 0·02''' and more) nerve-cells, all caudate, which are so irregularly imbedded among the longitudinal and transverse fibres, as to require no detailed description, and are connected on the one side with the grey nuclei of the *medulla oblongata,* and on the other with the *substantia nigra* of the *crura cerebri.*

The relations of the ten *pairs of nerves* which arise from the *medulla oblongata,* the *pons,* and the *crura,* constitute a very difficult question. But few inquirers have endeavoured to solve it by other means than those usually employed, that is to say, by the tracing of the fibres, with the aid of the scalpel,

Fig. 147. Nerve-cells of the *substantia ferruginea* in the floor of the fourth ventricle or rhomboid fossa, of Man, × 350 diam.

which here goes no way at all. Among the exceptions are E. Weber (Art. 'Muscular Motion,' in Wagner's 'Handw. d. Phys.' III, 2, pp. 20—22), who made his examination in preparations, hardened by carbonate of potass; and Stilling, who pursued his by the microscopical examination of sections, similarly hardened by means of alcohol. My own results, obtained from preparations in chromic acid, which had been for the most part made transparent by soda, agree in almost every point with those of Stilling, which at all events, among all observations on the subject, have gone most deeply into the matter.

The nerves in question arise, without exception, not from the columns or fibrous substance, out of which they proceed, but all penetrate more or less deeply into the central parts, and all probably become connected, some not till they have decussated like the *trochleares*, with definite parts of the grey substance, which Stilling not inappropriately terms *nerve-nuclei* (*accessory nucleus*, for instance). It is the floor of the fourth ventricle, and of the aqueduct of Sylvius, which are more particularly concerned in this respect, since all the nerves above named, at least in part, extend to them. The more minute consideration of these relations may be seen in Stilling's Work, and in 'Mikroskop. Anatomie,' II, 1, pp. 458—462.

[Although a favorable judgment cannot be given upon Stilling and Wallach's work on the spinal cord, I am still very far from disposed to look down upon Stilling's anatomical writings in general, as would seem to have been the fashion for some time past. I am much rather of opinion, in which R. Wagner also coincides, that we have great reason to thank this author for his works on the *medulla oblongata* and *pons Varolii*; for although there are some things in them which cannot be maintained, and sufficient attention is not paid to the elementary constituents, still it cannot be denied that they contain a mass of important facts. I have tested, if not all, still the most important of Stilling's statements, and have found them almost all fully confirmed, and am therefore glad to take this opportunity of naming him, as the observer to whom we are indebted for the first accurate investigation of the course of the fibres in the central organs. I would also here,

add: 1. that in further investigations of this kind, chromic acid, or chromate of potass, is to be preferred to alcohol, particularly also when caustic soda is cautiously employed for the tracing of the course of the nerve-fibres in the grey substance thus rendered transparent; and, 2. that in conjunction with lower magnifying powers, the most powerful should be employed, and the relations of the elementary constituents should also be otherwise accurately investigated.

The question as to the *origin of the nerves* in the *medulla oblongata*, presents itself as one of the most difficult nature. Most anatomists have hitherto been content to trace the roots of the nerves as far as one or the other column; but this is not sufficient. All the nerves enter at least once, or even several times, into grey substance, in which and no where else are their origins to be sought for. Now, it must be confessed, that through Stilling's great pains, the fruits of which I can, as it may be said, fully confirm,—all the ten pairs of nerves at present under consideration have been traced in their roots as far as perfectly definite points of the grey substance; but now comes for the first time the further question: do they commence in these situations, or do they proceed beyond them? As true origins in the brain have never yet been seen with certainty by any one, there remains nothing but physiological analogies and reasons. As regards the former, we see in all the spinal nerves, that they first penetrate transversely as far as the grey substance, and then, only passing through this, join the white columns, and we may thence suppose that the cerebral nerves, which, in general, so closely resemble them, are in the same condition, and the more so, because these also at first penetrate transversely into the interior of the medulla, and the grey substance, with which they come in contact, corresponds with that of the cord. To this may be added also, that if we make the ten last cerebral nerves terminate in the grey substance, into which they may so readily be traced, the decussated influence of the parts above, upon them, which appears to be established by pathological phenomena, cannot be explained in the case of any one of them except the *trochlearis*, which decussates before it reaches its grey substance. Now, in the *accessorius* and *hypoglossus* it is actually possible to see that the fibres come out from the grey

substance, reached by them in the first instance, and afterwards decussate; and the same thing is also at least probable in the *oculo-motorius;* so that I think it may be, that all the nerves now in question undergo decussation, and do not terminate in the so termed nuclei of Stilling. Further investigation will have to show whether this [decussation] takes place in the floor of the fourth ventricle, as would appear to be the case; whether all the fibres of these nerves take part in it; and where the fibres proceed to after decussation. With respect to the latter, it may be supposed from analogy with the spinal nerves, that the true origin of the cerebral nerves is probably not in the *medulla oblongata*, but in the *corpora striata* and *optic thalami*. Of that portion of the *portio major n. trigemini*, which is continued into the restiform body, this may especially be remarked, that it certainly does not originate in that part, but winds round it to somewhere above, as is the case also with the *n. accessorius*.

However, in stating, in accordance with what has been said, that I do not consider it directly probable, that the sensitive and motor cerebral nerves originate in the *medulla oblongata* and *pons*, it is by no means intended to imply that these parts may not, as central organs, exert some influence upon them and the more deeply placed nerves. If the *medulla oblongata* preside over the respiratory movements, if it and the *pons* be the agents of multiplied reflex motions, this may be the case, without its following that all the nerves called into action should terminate in them, and simply for the reason that the grey substance, so abundantly contained in them influences the nerves which traverse it, exactly as must be supposed to be the case in the spinal-cord.]

§ 115.

The *cerebellum*, with respect to the distribution of the elementary tissues, exhibits tolerably simple conditions, grey substance occurring only on the surface of the convolutions, in the *nucleus dentatus*, and in the roof of the fourth ventricle; all the remainder consists of white substance. The latter is wholly constituted of parallel, probably unbranched, dark-bordered nerve-fibres, possessing all the characters of central fibres (softness, proneness to become varicose, easy isolation of the

axis-cylinder, &c.), are essentially alike in all situations, as far as their condition can be observed, and present a diameter of 0·0012—0·004‴ in the extremes, and of 0·002‴ in the mean. The *grey substance* occurs, in the first place, very scantily in the roof of the fourth ventricle above the *velum medullare inferius*, in the form of brown nerve-cells, measuring 0·02—0·03‴, scattered in the white substance, and recognisable by a sharp eye without further aid, (the *substantia ferruginea superior*); and, secondly, in the *nucleus dentatus*, the greyish red lamella of which contains a considerable number of yellowish pigment nerve-cells of a medium size (0·008—0·016‴), with four or five processes, and which have no direct connection with numerous nerve-fibres proceeding from the *nucleus dentatus* into the medullary substance of the hemispheres, which pass through among them.

The relations of the *grey substance on the surface of the convolutions* of the cerebellum are more complex, (*vide* 'Mikrosk. Anatomie,' Pl. IV, fig. 4). It consists everywhere, as is well known, of a layer, internally of a rusty colour, externally grey, which, except in the fissures, where the internal layer is most usually thicker, present pretty nearly the same, but not everywhere an equal thickness.

The internal *ferrugineous layer* contains nerve-fibres and large masses of free nuclei. The former arise, without exception, from the white substance, and run, in general, parallel to each other, although on a transverse section of any convolution slightly diverging in a penicillar manner, directly into the ferrugineous layer. Within this layer they also run from within to without as far as the grey layer, but are broken up into numerous, for the most part, fine fasciculi, which are much interlaced, so that the whole ferrugineous layer is penetrated by a close but delicate network of nerve-fibres, which recalls in appearance the terminal plexuses in peripheral parts, as, for instance, in the *n. acusticus*, in the follicles of the *vibrissæ*, &c. In the meshes formed by these nerve-fibres lie a vast number of opaque, round corpuscles, measuring 0·002—0·004‴, in the mean 0·003‴, which are nothing else than *free nuclei*, and which frequently also exhibit a distinct nucleolus, and not unfrequently other granules.

In their passage through the ferrugineous layer, the nerve-

fibres of the white substance become gradually attenuated, most of them to a diameter of 0·0012‴, and in this state enter the external *grey layer*. This layer, although to outward appearance everywhere perfectly homogeneous, consists of two, not well defined laminæ, the inner of which contains nerve-fibres and very well marked, large nerve-cells, whilst the outer presents nothing but a finely granular, pale, light yellowish substance, which is distributed generally throughout this grey layer, and contains no nerve-cells. The *granular substance* agrees chemically, morphologically, and physically in all respects with the already described contents of the nerve-cell; it is tenacious, elastic, rendered more opaque by acetic acid, and more transparent in caustic soda, in which it is, for the most part, dissolved, and exists in the purest form in the outer half of the grey layer, that is to say next to the *pia mater*. The *small nerve-cells*, speaking generally, are very few in number and indistinct. They occur scattered throughout the grey layer, having a diameter of 0·004—0·008‴, more frequent towards the ferrugineous layer than more externally, and when successfully prepared, particularly by means of chromic acid, most of them exhibit delicate processes, which, however, can never be traced to any distance, and are frequently torn off close to the cells. Besides these cells, there also occur here and there, but on the whole rarely, nuclei of 0·002—0·0048‴, which, to all appearance, are free, as they are met with even in the most carefully made preparations. Entirely different from these smaller elements, and very peculiar, are the *large cells* of the grey layer (fig. 148) discovered by Purkinje. These cells, measuring 0·016—0·03‴, and of a round, pyriform, or oval figure, with finely granular, colourless contents, occur only in the innermost portions of the grey, close to the ferrugineous layer, and they are, not unfrequently, at least some of them, partly imbedded in its nuclei, in single or multiple layers, and presenting 2—3, rarely 1—4, long and much branched processes, directed particularly towards the outer surface of the convolutions, which are, almost without exception, at all events the strongest of them, given off from the sides of the cells which look from the ferrugineous layer. At their origin these processes are even 0·007, or as much as 0·008‴, thick, and extremely finely granular or very delicately

striped. As they proceed they become more homogeneous, and at the same time divide into very numerous and extremely

Fig. 148.

slender branches, so that at last, from each process a large bundle of very fine filaments, having a diameter, in the finest, of scarcely 0·0002‴, is produced. A portion of these fibrils penetrate more horizontally into the grey layer, although most of them stretch directly outwards, and appear to extend nearly to the outer surface of the grey layer. That they extend very far is certain, for in preparations made with chromic acid, I have isolated some measuring 0·15—0·2‴, which were still not the finest; and in successful perpendicular sections through the cortical layers of the convolutions, their principal branches appear as parallel, slightly undulating fibres in close contiguity, extending through more than two thirds, or even three fourths, of the grey layer, to which they give a peculiar striated aspect. Whilst the principal prolongations of the processes are, in this way, continued through the grey layer, they give off their branches at acute or right angles, whence not unfrequently a second striation is produced, crossing the one just described at a greater or less angle.

In the innermost portion of the grey layer, among the large

Fig. 148. Large cells of the grey layer of the cortical substance of the human cerebellum, × 350 diam.

cells, there moreover exist some *nerve-fibres;* but which, owing to their delicacy and the ease with which they are destroyed, it is very difficult to trace. Quitting the ferrugineous layer, and forming a continuous plexus, they are distributed in the inner third of the grey lamina among the large cells and their processes; their mode of termination has escaped my observation, the result of which amounts only to this: 1. that they become finer and paler, decreasing from their original thickness of 0·0012‴, ultimately to one of 0·0006‴ and 0·0004‴, their dark outlines also being replaced by a paler contour; 2. that they certainly do not form terminal loops, such as Valentin and Hyrtl, who have probably mistaken a fine plexus for such, think they have noticed; but becoming isolated, and running in a more straight direction, and almost as pale as the processes of the nerve-cells at the border of the inner third of the grey lamina, are lost towards the middle of it.

The *crura cerebelli* are composed of nothing but parallel nerve-fibres, without any admixture of grey substance, corresponding with those of the medullary substance of the *cerebellum* itself, as a continuation of which they are to be regarded.

§ 116.

Ganglia of the Cerebrum.—The three pairs of cerebral ganglia, the *corpora quadrigemina, optic thalami,* and *corpora striata,* all consist of bulky collections of grey substance, and of nerve-fibres; the former of which are in part quite isolated (*corpus striatum*), in part mutually connected, and with more deeply lying portions of grey substance (*thalami optici, corp. quadrigemina*); the latter connect the ganglia, on the one hand, with the *cerebellum* and *medulla oblongata,* and on the other with the hemispheres of the cerebrum.

The *corpus striatum* contains two large grey nuclei, the *nucleus caudatus* anteriorly and superiorly, and the *n. lenticularis* posteriorly and inferiorly, which are, however, connected in front, constituting a single mass; and besides these, the slender *n. tæniæformis,* with the *amygdalæ* external to the lenticular nucleus, and is in connection principally with the basis of the cerebral peduncle or continuation of the pyramid,

which expands in it, forming numerous white fasciculi. The *grey substance* presents, as almost universally, *nerve-cells* and fine *nerve-fibres*. The former, which measure from 0·006—0·018‴, are, in part, colourless, and in part, contain pigment, as, especially, in the caudate nucleus and third segment of the lenticular nucleus; they are furnished with from two to five processes, and occur in greater numbers according to the depth of colour of the grey substance.

The *nerve-fibres* may be referred for the most part to those of the basis of the *crura cerebri*. They present the form of dark-bordered tubes from 0·0012—0·005‴, most of them from 0·002—0·004‴ in size, which, running parallel and close together in a straight direction, enter the first division of the lenticular nucleus, and the most anterior, thickest portion of the caudate nucleus. When traced further in the lenticular nucleus, it will be seen that they form larger and smaller fasciculi, decreasing somewhat in size (most of them measuring from 0·0012—0·003‴; and that, passing straight through the more scanty grey substance of the first divisions of the lenticular núcleus, they are all ultimately lost, spreading out in a penicillar form in its outermost and largest division. That is to say, white fasciculi measuring from 0·04—014‴, with fibres of 0·0012—0·002‴, enter this division of the nucleus from the second; and these fasciculi in close contiguity, slightly diverging and subdividing into smaller bundles, are continued further in a direction towards the outer border of the lenticular nucleus, before reaching which they disappear to the naked eye. If traced microscopically in preparations made with chromic acid, it is apparent, that the fasciculi proceed nearly to the outermost part of the lenticular nucleus, though gradually broken up into smaller bundles and separate fibres, and most intricately interlaced with each other. *That these fibres terminate here, and do not proceed any further into the medullary substance of the hemispheres, may be considered as made out,* not the faintest indication of any further continuation being afforded, which, if it existed, could not escape being seen; on the other hand it is doubtful *how* they terminate here. All I have to state on the point is this: that the fibres of the nerve-fasciculi, entering the third division of the lenticular nucleus, as may be directly observed in a very great

many instances, gradually become so much attenuated, as ultimately to measure not more than 0·0008‴, 0·0006‴, or even hardly 0·0004‴, and present an almost entirely pale aspect, so that they can scarcely any longer be distinguished from the finer processes of the nerve-cells; with which in fact, unless everything is deceptive, they most probably are actually connected. All the fibres, also, which enter the caudate nucleus, present exactly the same conditions; some of these enter the nucleus directly from the basis of the cerebral peduncle, others, which appear in its thinner portion, are manifestly derived from the lenticular nucleus, the first two divisions of which they traverse in the first instance; in this case, also, there is no transition of the fibres into the medullary substance of the hemispheres, but a separation of the fasciculi into a plexus of the finest, almost non-medullated fibres takes place, and probably a connection between them and the cells.

Besides the above described, in any case very numerous, nerve-fibres derived from the cerebral peduncles and terminating in the *corpora striata*, the nuclei of those bodies contain a considerable number of other fibres, whose origin it is, in part, difficult, and, in part, impossible to assign. I think I can trace one set of these fibres to their source. In the most external part of the large nucleus of the *corpus striatum*, we find, on making various sections, a considerable number of moderately strong fasciculi, though not visible to the naked eye, which in their relative thickness and the diameter of their tubes (0·0012—0·002‴) differ from the fibres derived from the *crus cerebri*, which in this situation are reduced to the most extreme attenuation and dispersed in a plexiform manner. It is easily seen, that all these fasciculi proceed from the medullary substance of the hemispheres; and, as it appears, after they have run a certain distance parallel with the surface on the border of the nucleus of the *corpus striatum*, that they enter it. Many of these fibres are continued directly from the medullary substance into the ganglia, and, in this way, decussate, at right angles, with the former fibres. Assembled in fasciculi, these fibres penetrate more or less deeply into the grey substance of the *corpus striatum*, and of the third division of the lenticular nucleus; and these terminate, as I think I have observed, without any considerable expansion, the formation of a plexus,

or undergoing any farther decrease in size, their fibres forming loops with closely approximated sides.

Although, speaking relatively, it is not difficult to make out the structure of the *corpus striatum,* at all events, in its principal features, it is quite otherwise with the *optic thalami* and *corpora quadrigemina,* chiefly because the nerve-fibres in these situations are not so much assembled into fasciculi, but are more isolated and most intimately intermixed with the grey substance, on which account they cannot be traced to any great distance. The examination of the grey substance itself, however, is perfectly easy even in these bodies, and its elements —the nerve-cells—present nothing peculiar, except that, in the optic thalami, they are for the most part more deeply coloured, whilst those in the *corpora quadrigemina* are paler. With respect to the nerve-fibres, it is quite certain that the superior portion of the *crura cerebri,* that is to say, the *crura cerebelli ad corpora quadrigemina,* the continuations of the olivary columns, portions of the *corpora restiformia,* and the *eminentiæ teretes,* pass into the ganglia now under consideration, although I have not as yet succeeded in eliciting anything determinate as to the course they take. But I think it may be stated, that the fibrous masses above named, in great part at least, are not continued into the medullary substance of the hemispheres, because, on the one hand, most of their fibres decrease from the original diameter of 0·0012—0·004‴ down to the smallest, or less than 0·001‴; and on the other, because no such passage of the fibres can be perceived on that side of the optic thalamus, which looks towards the medullary substance of the hemispheres. The superficial white investment, however, of the ganglia in question, must be excepted, which in any case may effect a relation between them and the hemispheres, as its fibres, measuring 0·001—0·003‴, or even more, disposed in fasciculi, and crossing each other horizontally in various directions, do not appear to terminate in it. Neither is the relation of the optic thalami to the *corpora quadrigemina,* and that of the *fornix* to the latter, by any means clear, so that it is pleasing, at all events, to find that another important question admits of a more satisfactory solution. When the external portion of the optic thalamus is examined, it will be found that it adjoins a considerable mass of white substance, which

at first sight appears to be a continuation of the basis of the cerebral peduncles passing below and external to the optic thalamus, between the lenticular and caudate nuclei of the *corpus striatum*, to enter directly into the medullary substance of the hemispheres. Closer observation renders it obvious, that this white substance, as has been said before, in part enters the *corpus striatum*, particularly the lenticular nucleus, and in part radiates from without inwards, *from the hemisphere into the optic thalamus*. That is to say, very numerous white fasciculi, visible even to the naked eye, coming from the hemisphere throughout the entire height of the thalamus, enter the latter, run towards the superior surface to the superior and internal border, and the *pulvinar*, being ultimately lost exactly in the same way as are the fibres continued from the *crus cerebri* into the *corpus striatum;* that is, these fasciculi, the elementary fibres of which originally measure 0·0012—0·0025‴, ultimately subdivide into extremely close plexuses composed of fibres of the most extreme fineness, 0·0004—0·0008‴, the terminations of which cannot be traced.

I will just notice the constitution of some structures connected with the above-described ganglia. The *substantia nigra* of the *crus cerebri* presents pigment-cells precisely similar to those of the *substantia ferruginea*, except that they are for the most part rather smaller, and have fewer processes, surrounded with nerve-fibres of the finest, and also of the stronger kind. The *commissura mollis* contains smaller cells, with 1, 2, 3, and more processes, and light coloured pigmentary contents; and besides these, very many, plexiform, vertical, and horizontal, fine fibres of 0·0012—0·0016‴, with some still finer, less than 0·001‴, and a few stronger measuring as much as 0·004‴. The *pineal gland* exhibits pale, rounded cells, without any processes, and scattered nerve-fibres of 0·001—0·002‴, and also, generally, a considerable quantity of sabulous matter (brain-sand) (*vid.* § 118). Its peduncles, their anterior prolongations, and the *commissura posterior*, contain fibres measuring 0·001—0·003‴, and are composed in part also of the finest fibres. The *floor of the third ventricle* presents, immediately beneath and behind the anterior commissure, extremely large, and smaller, colourless cells, with from one to four, occasionally very thick processes. These are lodged in great

number in a close plexus of fine fibres of 0·0004—0·0012‴; and cells, in other respects exactly similar, though not quite of the same size, also exist in the *corpus mammillare*, likewise intermixed with very numerous fibres of the finest sort; there are other still smaller cells of 0·008—0·012‴, for the most part with only two processes, in the *tuber cinereum*. The *hypophysis cerebri* contains, in its anterior, reddish lobe, no nervous elements; but rather, according to Ecker (art. 'Blood-vascular Glands,' in Wagner, 'Handw. d. Physiol.'), the elementary tissues of a blood-vascular gland; that is to say, a vascular stroma of connective tissue, in the interstices of which, lie vesicles (cells?) measuring 0·030—0·090 ^{mm}, containing sometimes only nuclei, and a fine granular substance, sometimes distinct cells, in older persons also colloid-like masses. The posterior, smaller lobe consists of a fine granular substance, with nuclei and blood-vessels, and also contains fine, varicose nerve-fibres, which, like the vessels, descend from the *infundibulum*.

§ 117.

Hemispheres of the Cerebrum.—The white substance of the hemispheres of the brain consists entirely of nerve-fibres, of 0·0012—0·003‴, on the average 0·002‴ in size, without any admixture of grey substance. These fibres, of whose special course, we, as yet, know extremely little, never form plexiform interlacements or fasciculi, but all run in parallel, and most generally, straight lines, and undoubtedly proceed from the *corpus callosum* and ganglia of the cerebrum as far as the superficial grey substance, whilst it must remain undetermined whether, in their course, they divide or not. But besides these fibres, omitting also the *commissura anterior*, the *fornix*, and the origin of the optic nerves, the hemispheres contain others crossing the former at right angles. I have found these fibres, in the first place, on the outer side of the *corpus striatum*, in which situation they are to be referred, in part, to the fibres which enter the *corpus striatum* from the hemispheres and terminate in it; perhaps, also, in part, to the expansion of the *corpus callosum* in the inferior lobes; and secondly, in the most superficial layer of the white substance, near the grey cortical substance, where they occur in not

inconsiderable numbers, and running, in part, obliquely; but of their origin nothing satisfactory could be ascertained. Whether there are still other, and what traces of fibres, the future must show.

The more intimate structure of the *grey substance* of the convolutions, is tolerably manifest (*vid.* 'Mikroskop. Anatomie,' Pl. IV, fig. 2). It is most conveniently divided into three layers, an external, *white;* a middle, *pure grey;* and an internal, *yellowish red.* The latter, in thickness almost equal to the other two, usually presents, on its outermost border, a clear, frequently white streak, and occasionally, more internally, a second, thinner and less white layer, so that there are in fact four or even six successive laminæ: 1. a yellowish-red layer (inner part); 2. the first white streak; 3. yellowish-red layer (outer part); 4. second white streak; 5. the grey layer; 6. superficial white layer. The grey substance contains, in its whole thickness, both nerve-cells and nerve-fibres; and besides these, much granular matrix-substance, exactly like that of the cerebellum. The nerve-cells are not easily investigated, except in preparations in chromic acid, and in all the three layers they agree in this respect, that by far the greater number of them are furnished with from one to six processes, which give off numerous branches, and ultimately form extremely fine, pale fibrils of about 0·0004‴ in diameter, differing, however, in respect of size, number, &c. In the superficial white layer the cells are few, small (0·004—0·008‴), with one or two processes, and scattered in an abundant, finely granular matrix. The middle or pure grey layer, most abounds in cells, which in it, are closely aggregated also in a granular matrix. Their size varies very considerably, some being very small (0·003—0·005‴), frequently appearing as little more than nuclei, whilst there are many others of larger dimensions, up to 0·016‴ and 0·02‴ (fig. 149). Their figure is pyriform or fusiform, tri- or multangular, also perhaps more rounded, by far the greater number having from one to six processes, usually three, four, or five; and where this is not the case, they may have been torn off in the preparation, since stumps of them may be very readily noticed in the cells, which are altogether very delicate. In the innermost *yellowish-red* layer, lastly, the cells are again rather more scanty, though still

extremely abundant, otherwise presenting the same characters as those in the grey substance, having sometimes pale, sometimes pigmentary contents; the latter in the inner layers more particularly, and in old persons.

The *nerve-fibres* of the grey substance of the convolutions, arise, as it is easy to demonstrate, from the medullary substance

Fig. 149.

of the hemispheres, and penetrate, bundle after bundle, directly, and all parallel, into the yellowish-red layer. Arrived here, many fibres separate from the rest, and penetrate the yellowish-red layer in all directions, but more especially parallel to the surface, and consequently crossing the main fasciculi. When these horizontal fibres are more closely aggregated, they produce the above-described whiter or clearer streaks in this layer, the outer of which streaks is situated exactly at the point, where the fasciculi which enter the grey substance, are lost. In fact, as these proceed more outwardly, they constantly decrease in size, owing to their giving off lateral fibres, and to the attenuation and separation of their elements, until, when they have reached the grey layer, they become lost to sight, although if more closely traced they may still be

Fig. 149. From the internal portions of the grey layer of the convolutions of the human cerebrum, × 350 diam. Nerve-cells; *a*, larger; *b*, smaller; *c*, nerve-fibres with axis-cylinder.

perceived as intricately interlaced fibrils of the utmost fineness, and with scarcely any appearance of dark contours, only that there are a certain, though smaller number of fibres, which, upon reaching the grey layer, do not lose their breadth and dark contours, but are continued in a straight or oblique course through it, extending horizontally to a further distance, in the outer white layer. In this layer, consequently, we find a considerable number of finer, and of the very finest fibres (fig. 150), crossing each other in various directions, and in several superimposed layers, which are obviously, as to their origin, to be referred to those arising from the reddish-grey layer; and which probably also, as Remak has assumed, are derived, at the basis of the cerebrum, from the anterior extremity (knee) of the *corpus callosum*. How these fibres are related to the cells in the white layer is doubtful, although this much is certain, that many of them return into the grey-red substance from which they arose, or in other words form *loops*, which were first described by Valentin, and which I have very frequently and distinctly noticed in chromic acid preparations treated with caustic soda. I have also observed, in the grey-red substance, isolated loops with closely approximated sides, and also with their convexity looking towards the surface of the brain. The fasciculi of the grey-red substance contain fibres which, at first, measure 0·0012—0·003‴, but almost all of which ultimately decrease in size down to 0·001‴, and, in the grey substance, acquire the diameter of the smallest nerve-tubes, 0·0004—0·0008‴. The fibres given off from these

Fig. 150.

Fig. 150. Finest nerve-tubes of the superficial white substance of the human cerebrum, × 350 diam.

fasciculi within the grey-red layer are, in part, of the same size as those in the fasciculi,—which is the case particularly with those of the thicker white streak,—in part finer. The fibres which proceed from these fasciculi into the superficial white substance, are also, usually, of greater size, up to 0·003‴, many of which form loops; there are, however, in this layer together with these, some of the finest fibrils, measuring 0·0004‴. Notwithstanding all my endeavours, I have been unable to discover any connection between the nerve-cells and fibres, in the cortical portion of the *cerebrum;* but the existence of such a connection would appear to me to be nowhere so probable as here, where the nerve-fibres, especially in the pure grey layer, assume so much the appearance of processes of the cells, as almost to deceive the observer, and where, in any case, they terminate. There are in this situation an immense number of nerve-fibres, so fine and pale that they could scarcely be regarded as such, were they not straighter than the processes, and did they not, particularly when treated with soda, exhibit minute varicosities. If anywhere in the central organs, an origination of nerve-fibres exists here, although it is quite intelligible that it should not yet have been observed, when we consider the delicacy of the structures concerned.

The *corpus callosum* presents, in the anterior portions of its body above the *septum pellucidum*, the *fornix*, and the *corpora striata*, dull grey streaks, scattered in the white substance, in which the microscope discovers no cells, but only clear vesicles of 0·003—0·004‴ with nuclei, in the midst of numerous nerve-tubes, similar to what are met with in certain fasciculi of fibres of the *corpus striatum*. Besides this, Valentin ('Nervenl.,' p. 244) occasionally noticed on the surface of the *corpus callosum*, between the *raphe* and the *striæ obtectæ*, a delicate grey investment with clear nerve-cells, which appears to be identical with the *fasciola cinerea*, which is continued into the *fascia dentata* of the *pes hippocampi major* (*vid.* Arnold. 'Bemerk,' p. 87); otherwise the *corpus callosum* is wholly composed of white medullary substance with parallel nerve-fibres of exactly the same aspect and diameter as those of the medullary substance of the hemispheres. The same may be said, also, of the *commissura anterior* and *fornix*, which latter, however, comes in contact with grey substance in very many

ways, as in the optic thalamus, from the *tuberculum anteri* of which its *radix descendens* arises; in the *corpus mammilla* (*vid. sup.* § 116); at the commencement of the *radix ascendens* in the floor of the third ventricle, towards which some delicat fasciculi of the *radix ascendens* are given off; and at its poin of junction with the *septum pellucidum*, which latter, togethe with a common thick coat presenting much connective tissu and *corpuscula amylacea* (*vid.* § 118), exhibits numerou plexuses of the finest kind of nerve-fibres and nerve-cell exactly as does the *tuber cinereum*. The fibres of the *forni* measure, in its white portions 0·0008—0·005‴, mostly 0·002—0·003‴; in the *optic thalamus* (upper part), and in the *corpu mammillare*, the fibres are only of the finest sort, measurin 0·0004—0·001‴. The *cornu ammonis*, and the *calcar avi* (*pes hippocampi minor*), present nearly the same conditions a those of the cerebral convolutions; in the grey substance o the former, however, there is a peculiar sort of streak, contain ing chiefly round cells without processes, and closely aggregated

Lastly, we have to consider the origin of the first two pair of nerves. The *olfactory nerve* contains, in the white portion of the *tractus olfactorius*, fine nerve-fibres, of 0·0004‴, or at most 0·002‴, the finest, pale-bordered, and apparently non-medullated; and besides these, also some grey substance, with fine granular structure, and cells of 0·007—0·008‴. These cells, with some still smaller, down to a diameter of 0·003‴, many with branched processes, constitute the *bulbus n. olfactorii*, intermixed with numerous fine fibres, the relation of which to the cells and to the true nerves of smell cannot be made out. The *optic nerve* arises, with its *tractus* divided into two crura, from the *corpora geniculata*, and the *corpora quadrigemina* and *optic thalami*; besides which, it is also in connection with the *crura cerebri*, the *substantia perforata antica*, the *tuber cinereum*, and the *lamina terminalis*. The precise origin of its fibres, dark-bordered tubes of 0·002‴, is in Man unknown, but to draw conclusions from experiments in animals, it exists principally in the *corpora quadrigemina*, whilst we know that they partially decussate in the *chiasma* (commissure). In this body, however, there are, as stated by Arnold, Todd and Bowman, &c.: 1. fibres which do not decussate, but are continued from the *tractus* into the optic nerve of the same side; and 2. com-

missural fibres, which may indeed be divided into an anterior and posterior set, the latter constituting a commissure between the two points of origin of the optic nerves, whilst the anterior could only unite the two *retinæ*. The existence of the first-named fibres is certain, although they are much more scanty than the decussating elements; but that of the others also can hardly be denied. Speaking physiologically, a commissure of the optic thalami and *corpora quadrigemina* may perhaps be explained, but a commissure also of the *retinæ* does not appear to be altogether impossible, because we know that the *retina* contains grey substance, and in it, nerve-cells with branched processes.

[With respect to the *origin of the nerve-fibres* in the brain and higher central organs, in general, it is several years since I first observed the origin of dark-bordered fine fibres from the processes of the nerve-cells in the spinal cord of the Frog ('Zeitsch. f. wiss. Zool.,' vol. I, p. 144, tab. xi, fig. 7). In *man* I have not as yet been so fortunate as to perceive anything of the sort with certainty, though I do not myself doubt that similar conditions obtain in this case also. In fact, R. Wagner and Leuckart think they have seen, in man, the processes of the many-rayed cells in the *substantia ferruginea,* passing into nerve-tubes ('Gott. Anzeig.,' 1850, No. 43); as has Prof. Domrich, in the cortical substance of the *cerebellum,* according to a communication to me by letter. R. Wagner again ('Gött. Nachr.,' Oct. 1851), has, recently, also found in the electric lobes of the Ray, that from the many rayed ganglion-globules or nerve-cells, one, or more rarely two, unbranched processes are continued into dark-bordered fibres. He now explains this transition, in the same way as before, saying that the processes were continued as axis-cylinders into the dark-bordered tubes, in which Leydig, who has observed the same transition in the *cerebellum* of the "Hammer-headed Shark," agrees with him, as does Stannius, in the case of *Petromyzon*. Nevertheless, it is still not quite evident to me, that any condition should exist in this case, different from that which obtains in the ganglia, where the processes of the nerve-cells are not simply axis-cylinders, but also have a coat, which investing the medullary matter of the nerve, is continuous with the sheath of the dark-bordered tubes; although, seeing that the presence of tunics on

the nerve-corpuscles of the central organs, and their processes, in general, is still a disputed point, I am prepared to admit that the fact may be otherwise. These researches have opened the way, and I have no doubt, as I have already said in my Microscopical Anatomy, that in time we shall succeed in demonstrating the origin of dark-bordered tubes in many other situations in the central organs, in man, and other animals. On the other hand, however, supported by repeated investigation of the human brain, I must assert, that it is in the highest degree probable that in many places it will be altogether impossible to demonstrate the origin of fibres from nerve-cells, because very many nerve-tubes, particularly those of the cortical substance of the *cerebellum* and *cerebrum*, ultimately become so pale and slender, as not to allow of their being distinguished from the processes of nerve-cells. Whether the loops which distinctly exist in the convolutions of the *cerebrum*, and which I have also seen in the *corpora striata*, are terminations, or whether free prolongations of nerve-tubes exist, we know not, and the less so because it cannot even be asserted that certain fibres really do terminate. It may fairly be assumed that the fibres of the *corpus callosum* and the commissural fibres in general, commence in the one hemisphere in connection with cells and terminate in the other, and that the fibres which proceed from the surface of the convolutions to the optic thalami and *corpora striata* terminate in the latter, but to assert, that it is so, is impossible, notwithstanding the visible loops, for it may be that these latter are not terminations at all, and that the fibres in question are all in the one place and the other in connection with nerve-cells. That nerve-fibres should originate independently of any connection with cells would be contrary to all analogy, but in such an obscure subject we must always be prepared for much that is new, and be careful not wholly to reject any possibility, simply from *à priori* considerations. Several authors have noticed divisions of the nerve-tubes in the central organs, such as, among the older ones, Ehrenberg, Volkmann, E. H. Weber, and more lately also, Hessling ('Fror. N. Notiz.,' Ap. 1849, Jenaische, Ann. I, p. 283), E. Harless (ibid., p. 284), and Schaffner ('Zeits. f. rat. Med.,' IX) in the brain of various vertebrate animals, especially at the junction of the white and grey substance. I am not

inclined to doubt these statements, especially the latter, but I cannot avoid the remark, that in the human brain, I have, hitherto, in vain sought for divisions of this kind, and have had many hundreds of fibres from the grey substance before me, under the most favorable circumstances, which presented no indications of the sort, whilst I have invariably found such divisions in the spinal cord (*vid.* supra). The many rayed nerve-cells with branched processes are not as yet fully known in all their relations. I have described their processes, (as will be universally allowed, correctly,) as a sort of pale, non-medullated nerve-tubes, and have isolated them occasionally to the extent of $\frac{1}{5}$ and $\frac{1}{4}'''$, without being able to notice anything more with regard to their termination, than the fact of their ultimately assuming an extreme degree of fineness. R. Wagner states, that those processes, which do not pass into dark-bordered nerve-tubes, serve to connect the separate nerve-cells together, but in so doing he manifestly says more than actual observation warrants, as he has, hitherto, seen such a connection, only in the electric lobes of the Ray. In the present state of neural Anatomy there is nothing which should be more carefully avoided than the general application of isolated observations, and I am therefore of opinion that this question must as yet be regarded as an open one. It may indeed be very consonant with physiological considerations, to explain the reflex and alternating actions of separate sections of nerves by such connections between the cells, but it is precisely for that reason, that we should be the more careful, and the more so because less obvious theories explain the conditions just as well. I conclude, therefore, from the observations hitherto made, only this much, that nerve-cells may anastomose, leaving it to future inquiries to decide, whether they do so universally and with all their processes, or whether in certain situations the latter do not stretch out without any attachment, exerting a mutual influence and affecting the nerve-fibres simply by juxta-position, as appears to be the case in the large nerve-cells of the cord and the roots of the spinal nerves.]

§ 118.

Membranes and Vessels of the central Nervous System.—A. MEMBRANES. 1. Spinal cord. The *dura mater s. meninx*

fibrosa is a whitish yellow, occasionally glistening, firm, tolerably elastic membrane, consisting of parallel and mostly longitudinal fasciculi of connective tissue, and of a fine, elastic, fibrous network in almost equal proportions. The outer surface of the *dura mater* is, in front, where the membrane is always at least as thin again as behind, pretty closely united to the *fascia longitudinalis posterior* of the spinal column, free posteriorly and on the sides, and separated from the arches of the *vertebræ* and their *periosteum* by a space, occupied by a lax connective tissue with anastomosing fasciculi scarcely more than 0·004—0·005‴ thick (reticular connective tissue), containing a few elastic fibrils (convoluted and longitudinal), and round, fusiform and stellate nucleated cells, similar to the formative cells of the connective tissue, and besides these with larger or smaller aggregations of frequently gelatiniform, transparent fat with cells containing serous fluid. The vessels of this space are in part the well-known *plexus venosi,* in part finer vessels, and also a network of the finest capillaries in the lax connective tissue itself. The internal surface of the *dura mater* would appear, from what is generally stated, to be lined with an outer lamella of the arachnoid; nothing however is to be seen but an *epithelium,* composed of polygonal, flattened, nucleated cells, on the innermost layer of the dura mater, and not a trace of any special substratum. The *ligamentum denticulatum* has no epithelium, and like the thickened processes of the *pia mater,* to which it is attached, presents, in all respects, a structure similar to that of the *dura mater.*

The *arachnoid membrane* is constituted, not of an external and internal lamella, the former of which is united to the *dura mater,* the latter free, but of a single layer corresponding to the internal lamella of authors. It is an extremely delicate, transparent membrane, exactly corresponding in extent and relations to the *dura mater.* Its outer surface, in the posterior mesial line of the cervical portion, is connected with the *dura mater,* above, by tolerably strong processes, lower down, by delicate fibrils, elsewhere it is perfectly smooth and glistening, which appearance depends upon an epithelium precisely like that of the *dura mater,* and it is merely in apposition with that membrane, as the pulmonary pleura is with the costal. The internal surface of the arachnoid is also smooth, though without

epithelium; it is separated from the spinal cord, and *cauda equina* by a large interspace, the *subarachnoid space*, affording, however, numerous slender processes to the *pia mater* and the roots of the nerves, which processes not only accompany the vessels and nerves, but occur, especially in the posterior mesial line, arranged in a consecutive series, and occasionally, particularly in the cervical region, form a perforated or complete septum. As regards its intimate structure, the arachnoid contains, chiefly, reticularly anastomosing bundles of connective tissue of 0·001—0·004‴, which are so united as to form lamellæ, some external with more slender, and some internal with stronger fasciculi, and which are usually so surrounded by fine elastic fibres, as to present a moniliform appearance when swollen by the application of acetic acid (fig. 23). In many fasciculi, these fibres are very fine or wanting, others again, in addition, contain elastic fibres also in the interior.

The *vascular membrane, pia mater,* very closely invests the spinal cord and the grey substance of the *filum terminale,* penetrating on the one hand into the anterior and posterior fissures, where it appears within the spinal cord in the form of slender processes, and affording, on the other, delicate sheaths to the roots of the nerves. It contains for the most part common connective tissue with straight fibres, and, more rarely, anastomosing bundles; and besides these a good many nuclei often of a lenticular form, with a few elastic fibrils. Here and there are met with in the *pia mater* bright yellow or brown pigment-cells, of an irregular, fusiform figure with fine prolonged ends and measuring 0·04—0·05‴ in length, which in the cervical region, owing to their greater number, give the membrane, not unfrequently, a brown or even blackish colour.

2. *Brain.*—The membranes of the brain, though corresponding, in general, with those of the spinal cord, yet present some differences. The *dura mater*, in this situation, consisting of the true fibrous membrane of that name and of the internal periosteum of the cranial bones, which, as the immediate continuations of the corresponding membranes of the spinal canal, become consolidated together at the level of the atlas, is, in general, thicker and also whiter than in the spinal cord. Its external or periosteal lamella, of a whitish yellow colour and rough, is attached more or less firmly to the bones, supports

the larger *vasa meningea,* and is also otherwise more richly supplied with vessels than the internal proper *dura mater,* with which, at an earlier period, it was more laxly united, and from which, except where the sinuses are contained, it may not unfrequently be separated even in the adult. The internal lamella is less vascular, whiter, presenting in many places a glistening tendinous aspect, and on its surface is quite smooth and for the most part even. The processes of the *dura mater,* the greater and less falciform processes, and the *tentorium,* appear as prolongations of this internal lamella; and between the two lamellæ are situated, with few exceptions, the venous canals or sinuses of the dura mater. Both lamellæ contain connective tissue of the same form as that in the tendons and ligaments, with, for the most part, indistinct bundles, and parallel fibrils, which either extend of a uniform size for considerable distances in it, or, especially as in the sinuses, form small, tendinous bands, crossing each other in various directions, and containing among them a good many fine elastic fibres. The internal surface of the *dura mater* is lined with a single (according to Henle with more than one) layer of tesselated epithelial cells, of 0·005—0·006‴ in size, with rounded or elongated nuclei measuring 0·002—0·004‴; possessing no other covering which might be described as a parietal lamella of the arachnoid (*vid.* Luschka, Seröse Häute, p. 64).

The *arachnoid membrane* of the brain differs from that of the spinal cord, not so much in its structure as in its disposition. It is true, that in this situation also, there is but one lamella demonstrable as a membrane composed of connective tissue, which corresponds with the so-termed visceral layer of the arachnoid of authors, and is also very closely applied to the inner surface of the *dura mater,* but the arachnoid membrane here is in much more intimate relation to the *pia mater.* That is to say, instead of its being united with the latter, as in the cord, by scattered fibres and lamellæ, it is, in the brain, in many situations, as on all the convolutions, and the projecting parts at the base of the brain, adherent to and coalescent with it, and, elsewhere, where this is not the case, united to it by numerous processes. For this reason, there exists, in the brain, no continuous subarachnoid space, but numerous, larger and smaller spaces, which only partially communicate. The larger

of these spaces between the *cerebellum* and *medulla oblongata*, and under the *pons Varolii*, the *crura cerebri*, the *fossa Sylvii*, &c., open directly into the subarachnoid space of the spinal cord, whilst the smaller, corresponding to the *sulci*, and over which the membrane composed of connective tissue is stretched, are perhaps partially in communication with each other, but, at all events most of them, not with the larger spaces just mentioned. The arachnoid, as has been correctly stated by Henle, is nowhere in connection with the lining membranes of the cerebral ventricles. The structure of the membrane is the same as in the spinal cord, except that the anastomosing fasciculi and spiral elastic fibres are for the most part thicker, measuring as much as 0·01‴ or even 0·02‴; and the former frequently present, as it were, special and more homogeneous sheaths of connective tissue, beneath which, fat- and pigment-granules are often deposited. The outer surface is covered with an epithelium in all respects like that of the *dura mater*.

The *pia mater cerebri* is more vascular but more delicate than that of the spinal cord, and covers all the elevations and depressions on the surface of the brain, if not very closely yet quite exactly, with the single exception of the floor of the fourth ventricle, above which it is stretched across from the *calamus scriptorius*, as far as the *nodulus*, the free border of the *vela medullaria inferiora* and the *flocculi*, forming the *tela chorioidea inferior*, from which points it proceeds to invest the under surface of the inferior *vermiform process* and of the *tonsillæ*. The *pia mater* penetrates into the interior of the brain only at one point, viz. at the transverse fissure of the cerebrum, where it passes beneath the *splenium corporis callosi*, investing the *vena magna Galeni* as well as the pineal gland, forming the *tela chorioidea superior*, with the *plexus chorioideus ventriculi tertii*; and passing beneath the *fornix*, also constitutes the vascular plexuses of the lateral ventricles, which are continuous with the *pia mater* at the base of the brain, between the *crus cerebri* and the inferior lobe. With respect to its intimate structure, the cerebral *pia mater* contains so many vessels, that in parts the connective tissue which forms the matrix appears as a subordinate constituent. It is rarely, as in the spinal cord, distinctly fibrous, for the most part more homogeneous, approaching in character 'Reichert's membranes,' or immature connective

tissue, with a few nuclei and without elastic fibres. Occasionally, however, the *pia mater* also contains reticular connective tissue, as around the *vena Galeni*, the pineal gland, the larger vessels, and also on the *cerebellum*. Fusiform pigment-cells also occur here, as in the spinal cord, particularly on the *medulla oblongata*, and *pons Varolii*, but also, more anteriorly, at the base of the brain as far as within the fissure of Sylvius, in which situation I have noticed them even in the *m. adventitia* of smaller arteries.

Those portions of the *pia mater* which are in relation with the ventricles, the *telæ chorioideæ* and *plexus chorioidei*, do not differ in their structure from other portions of the membrane, except that, especially in the *plexus*, they are composed almost wholly of vessels, and are furnished with an epithelium at those points where they are not adherent to the walls of the ventricles. This epithelium consists of a single layer of roundish polygonal cells, 0·008—0·01‴ in diameter, and 0·003—0·004‴ in thickness, and usually containing, together with the rounded nucleus, yellowish granules, often in great numbers, and one or two, dark, round oil-drops of 0·001—0·002‴ in size. According to Henle, almost all these cells send out, from the angles towards the layer of connective tissue of the *plexus*, short, slender, acuminate, transparent, and colourless processes, like spines; and according to Valentin ('Physiol.,' 2d ed., part 2, p. 22), in the Mammalia they also support cilia. The epithelium is succeeded by a thin layer of apparently homogeneous, connective tissue, beneath which is a very close interlacement of larger and smaller vessels, between which no formed connective tissue can be perceived, but only a clear, homogeneous, interstitial substance.

All the portions of the ventricles which are not lined by the continuations of the *pia mater*, that is to say, the floor of the fourth ventricle, the *aqueductus Sylvii*, the floor and the sides of the third ventricle, the *ventriculus septi lucidi*, the roof of the lateral ventricles, the anterior and the posterior *cornua*, and a considerable part of the descending *cornu*, in the embryo also the cavity in the olfactory bulb, and the canal in the spinal cord, have a special lining membrane, the so-termed *ependyma ventriculorum* (fig. 151). This is a simple tesselated epithelium, which, according to Purkinje and Valentin (Müll. 'Arch.,'

1836; Val. 'Repert.,' 1836, p. 156) is said to exhibit ciliary motion, a statement, however, which Virchow and I have not been able to confirm, in the case of an executed criminal. It lies, normally, immediately upon the nerve-substance, but there is so frequently developed beneath it, especially in the *fornix*, the *stria cornea*, and the *septum lucidum*, a filamentous layer, resembling connective tissue, 0·01—0·05''' thick, that its occurrence at a certain age might almost be described as constant, as in fact it is by Virchow. The epithelium sometimes presents, particularly as in the third ventricle, large cells of 0·008—0·012''', with pigment-granules and masses, together with nuclei, measuring 0·003'''; in other situations, as in the lateral ventricles, the cells are not more than 0·005—0·007''' in size, but almost as thick as wide, with roundish nuclei and a good many yellowish granules, which are generally crowded in the interior.

Fig. 151.

The vessels of the membranes just described present very various conditions. In the first place, in the *dura mater* of the cord, if we except those on the external surface and the numerous arteries and veins of the cord by which it is perforated —the vessels are very few in number, and in this respect the membrane presents more of the conditions of a muscular fascia or tendinous expansion. On the other hand, there exist in this situation, between the *dura mater* and *periosteum* of the vertebral canal, the well-known *venous plexuses*, as well as finer ramifications in the adipose tissue, which do not demand any further description. In the *cranium*, on the contrary, the entire *dura mater* is vascular, but especially in its external periosteal layer, which, partly for its own supply, partly for that of the cranial bones, to which it gives off numerous branches, supports the *arteriæ meningeæ*, and also conveys through its veins a portion of the blood returned from the bones. Besides this, in the cerebral dura mater are lodged the

Fig. 151. *Ependyma* in Man. *A*, from the *corpus striatum*; 1, from the surface; 2, from the side; *a*, epithelial cells; *b*, nerve-fibres lying beneath: *B*, epithelium cells from the *commissura mollis*: × 350 diam.

venous sinuses, which are simple excavations in it, for the conveyance of blood and lined with an epithelium; and most of which are obviously situated between the periosteal lamella and the proper dura mater, thus, in their position, corresponding with the *plexus venosi spinales*. The arachnoid membrane, either of the spinal cord or of the brain, contains no proper vessels (*vid.* Luschka, l. c., p. 71), whilst the *pia mater* in both situations supports not only the very copious ramifications of the vessels of the nervous substance itself, but is also supplied, with a tolerably rich, proper capillary plexus of its own. In one portion of the *pia mater*, viz. in the vascular plexuses, the vessels are distributed solely in the membrane itself, the branches entering the nervous substance being of subordinate importance. Lymphatics it is said have recently been injected with air and quicksilver by Fohmann and Arnold, (*vid.* 'Anat.' II, p. 618) both in the *pia mater* on the surface of the *cerebrum* and *cerebellum*, as well as in the choroid plexus, but this observation appears to me very much to demand confirmation.

The membranes of the central nervous system, also contain *nerves*, at all events in part. In the *dura mater* of the *cerebrum* they run in the periosteal lamella of the membrane, following pretty nearly the course of the meningeal arteries, and are especially distinct on the *a. meningea media*, which is accompanied, not only by twigs of the *nervi molles*, but also by a special nerve first noticed by Arnold (*n. spinosus*, Luschka), which, according to Luschka, is derived from the third branch of the *n. trigeminus*, the former of which are distributed with the vessels, and the latter appears to be destined principally for the bones. Besides these, Purkinje has noticed nerves on the anterior and posterior meningeal arteries, and Arnold long ago described the well-known *n. tentorii cerebelli*, proceeding from the fifth pair, which, as has been lately shown, particularly by Pappenheim and Luschka (l. c.), goes to the larger sinuses of the *dura mater*. The elements of this white looking nerve and of the *n. spinosus* of Luschka, are those of the *n. trigeminus*, those of the others, fine fibres, and in both situations they present divisions. In the *dura mater* of the spinal cord, I, as well as Purkinje, have been unable to detect any nerves; they occur, however, as has been already mentioned, in the periosteum of the vertebral canal, and on the arteries going to the

vertebræ and cord, as well as in the sinuses and lax adipose tissue of the canal (Luschka, l. c.).

In the *arachnoid* itself I have never noticed any nerves, but on the vessels by which it is penetrated, and in the processes connecting it with the pia mater, they may perhaps be seen, especially at the base of the brain—to which nerves, those seen by Luschka (Seröse Häute, p. 70), notwithstanding the divisions observed in them, appear to me to belong. Bochdalek (l. i. c.) has lately described nerves of the cerebral arachnoid, derived from the *n. accessorius*, the *portio minor trigemini*, and the facial nerve, but fails to show that they terminate in the membrane. When the same author also finds extremely numerous nerves in the arachnoid covering the *cauda equina*, he falls into the same error, as Rainey had previously encountered in regarding connective tissue, disposed in the more rare reticular form, as nerves. In the *cauda equina*, I am acquainted with nerves only on the *filum terminale*, accompanying the vessels, and nowhere else; not even in the dura mater, into which Bochdalek equally supposes he has traced them.

The nerves discovered by Purkinje in the *pia mater* of the Ox, also exist in man, in whom the pia mater of the cord, including the *filum terminale*, is richly supplied with plexuses of fine nerves, measuring 0·0015—0·003‴, which throughout do little more than accompany the vessels. At the base of the brain, many similar plexuses occur on the arteries of the circle of Willis, which, in twigs, at most 0·03‴ in diameter, are distributed through the entire pia mater of the brain, accompanying and always following the course of the various vessels, with the exception of those of the *cerebellum;* their terminations, however, can nowhere be perceived. It is certain that they do not accompany the arteries into the cerebral substance, and that no nerves exist in the vascular plexuses; whether there are any or not on the *vena Galeni*, I have not yet inquired. The origin of these nerves has been ascertained by Remak to be in the posterior roots, each of which, as I have satisfied myself, in many situations, and as it appears to me more frequently in the cervical portion of the cord, from the fibres in closest contiguity to each other, sends out fine fibrils across the subarachnoid space into the *pia mater*. As in this case, so also in the *cerebrum*, besides the sympathetic nerves (*plexus caroticus*

internus, plexus vertebralis), the cerebral nerves may participate in the supplying of the *pia mater*, since Bochdalek has noticed numerous fine twigs, given off from the roots of many of the cerebral nerves, of the same structure as the roots themselves, joining the nervous plexuses of the arteries at the base of the brain and of the *pia mater* of that region, and of the *cerebellum*, as well as in the plexus *chorioideus ventric. quart.* (?). He also found that isolated fine filaments entered the *pia mater*, directly from the *medulla oblongata*, the *pons Varolii*, and *crura cerebri*, which were not previously conjoined with the neighbouring nervous trunks.

B. *Vessels of the central nervous system.*—With respect to the distribution and condition of the blood-vessels—the brain and spinal cord agree almost entirely. After ramifying to a considerable extent in the *pia mater*, the arteries enter the nervous substance, except in a few situations (*substantiæ perforatæ, pons*), as fine, though still distinct, arterial vessels, and ultimately subdivide, by continuous ramification, for the most part at acute angles into a rather wide network of very fine capillaries, from which again the venous radicles arise, joining so as to form the well known trunks, both on the surface and in the interior (fig. 152). The grey substance is invariably much more richly supplied with vessels than the white, the plexus formed by them being closer, and the capillary vessels themselves of less calibre, to which its colour is in some respect due. According to E. H. Weber, the interstices of the capillaries in the medullary substance, measure 0·0142‴ in width and 0·025‴ in length; in an injected preparation by

Fig. 152.

Fig. 152. Vessels of the cerebral substance of the Sheep, from one of Gerlach's injections: *a*, of the grey; *b*, of the white substance.

Gerlach of the Sheep's brain, the breadth of the interstices in the grey substance was three or four times less than in the white. In the spinal cord, the disposition of the entering trunks is sometimes very regularly in series. Two series of vessels of this kind exist in the bottom of the anterior fissure, which, from the processes of the *pia mater*, penetrate the grey substance on the right and left; whilst a third series corresponds to the posterior fissure, and others not unfrequently also to the roots and the processes of the *ligamentum denticulatum*. All these vessels enter the grey substance without undergoing any direct or considerable decrease in size, and there find their ultimate distribution. In the brain very delicate parallel vessels are met with in the grey substance of the *cerebellum*, less distinctly in the *cerebrum* and other parts. The structure of the vessels is, in general, the same as elsewhere. The arteries, upon their entrance into the nervous substance, possess three coats—the *tunica adventitia*, though resistant, is a thin and apparently quite homogeneous membrane; the *t. media* is purely muscular; and the *t. intima* formed of nothing but a very delicate elastic membrane, with openings, and well-marked fusiform epithelial cells. One after another of these coats is gradually lost, till, before the capillaries are reached, we find nothing but the *t. adventitia*, and scattered, transversely placed, elongated cells, with transverse nuclei and an epithelium; with which class of vessels are soon associated capillaries with a structureless membrane and few or more nuclei, sometimes of great minuteness, the finest measuring, in the cord, 0·0022‴, in the brain 0·002‴. Of the veins, the largest, for the most part, do not present a trace of smooth muscle, exhibiting nothing but connective tissue with nuclei, or fine elastic filaments and epithelium; in the smaller ones I have, occasionally, though very rarely, observed contractile elements.

In the ventricles of the brain there exists, under normal conditions, an extremely small quantity of clear serous fluid, which is manifestly secreted by the arterial plexuses, and which, probably aided by the ciliary movements, assists in the nutrition of the walls of the cavities. A second fluid, the *liquor cerebro-spinalis*, is contained in the subarachnoid spaces above described, which, according to Luschka, are lined by an epithelium, and from the largest of which, extending from the

base of the brain to the termination of the canal of the *dura mater medullæ*, the fluid in question may be readily obtained. It is alkaline, contains—of water 98·56—albumen and extractive matter 0·55—salts 0·84 per cent., principally chloride of sodium. Its principal function appears to be to conduce to the more free motion of the central nervous system, and to act as a regulator in the varying degrees of fulness of the vascular system.

[A few pathological points may here be referred to. The *ependyma ventriculorum* presents not only, as above mentioned, almost constantly in places, a thin fibrous substratum, but is frequently, especially in dropsy of the ventricles, and in old age, very much thickened by a layer of that kind. In either case it invariably contains, as was first mentioned by Purkinje, yellowish bodies, with concentric striæ of a round or biscuit shape, and not unlike starch granules. They are scarcely affected by acids, whilst in caustic alkali they become pale and gradually dissolve. I find these *corpuscula amylacea* (fig. 153), almost always on the fornix, the *stria cornea*, and *septum pellucidum*, and also elsewhere in the walls of the ventricles, as well as in the cortical substance of the brain, in the medullary substance of the cord, and in the *filum terminale;* in the first-mentioned situations they frequently occur in incredible quantity, close together, in the newly formed connective tissue, or between the nervous elements. That these bodies are a pathological product is certain, but not so of what they consist, or how they are formed, although everything indicates a nitrogenous substance, and a formation from successive deposits. In the *plexus chorioidei*, in the pineal gland, occasionally in the *pia mater* and *arachnoid* (also in the cord), and, although rarely, also in the walls of the ventricles, there is furthermore met with, as a constant, though pathological production,

Fig. 153.

Fig. 153. 1, "Brain-sand" from the pineal gland, in bundles of connective tissue; 2, *corpuscula amylacea* from the *ependyma* of Man; × 350 diam.

the gritty matter of the brain (brain-sand). It consists of roundish, simple or mulberry-shaped, opaque, mostly concentrically striated globules of 0·005—0·05‴, and together with them of angular bodies, of a stalactitic, clavate, or other irregular figure, with an uneven, botryoidal, scaly surface; and also in the form of simple, cylindrical, rigid fibres, either branched or reticular, and of fine particles. The brain-sand contains principally carbonate of lime, but also phosphate of lime and magnesia, and an organic substance, which after the salts have been removed, for the most part perfectly retains the figure of the concretion, that is to say, of a concentrically laminated pale body, or as clear fibres. It is quite certain that this brain-sand, when it assumes the form of elongated, branched, reticular bodies, is simply developed in the bundles of connective tissue (fig. 153), as, not unfrequently, in the pineal gland and in the membranes of the brain; in other cases it appears to be an independent incrustation on fibrinous concretions. Whilst cells impregnated with calcareous matter, which Remak ('Obs.,' p. 26) supposed them to be, according to Harless (Müll. 'Arch.,' 1845, p. 354), do not exist. Lastly, also, may be mentioned the *Pacchionian granulations* of the *pia mater*, and ossifications of the membranes. The former, which are situated principally on both sides of the *falx major*, on the *flocculi*, in the *choroid plexuses*, &c. consist chiefly of a tough fibrous substance, not unlike immature connective tissue, containing also undeveloped elastic tissue, and *corpuscula amylacea*. The latter, which are true osseous plates, occur sometimes on the inner surface of the cerebral *dura mater*, sometimes on the arachnoid, particularly of the *cauda equina*.]

PERIPHERAL NERVOUS SYSTEM.

§ 119.

Spinal nerves.—The thirty-one pairs of nerves springing from the spinal cord, arise, with few exceptions, by *anterior* and *posterior roots*. Receiving a delicate tunic from the *pia mater*, they converge, and are continued across the subarachnoid space, to perforate, independently of each other, the

arachnoid and *dura mater*, from the latter of which they obtain a firmer coat. Proceeding further, the posterior root forms its *ganglion*, by the deposition around and among its nerve-fibres, of ganglion-cells, which, to all appearance, give origin to special nerve-tubes, the *ganglionic fibres* of the *spinal-nerves*, each for the most part arising from a cell, and which have no further connection with the fibres of the posterior root passing through the ganglion, than that, in their invariably peripheral course, they are in apposition, and intermingled with the latter. The motor root never acquires ganglion-cells, merely passing by the ganglion, in more or less close apposition with it. Beyond the ganglion, the two roots are united in such a manner that their elements are very intimately commingled, and a common nervous trunk formed, containing in all its divisions sensitive and motor elements. It is usually connected with the neighbouring nerves above and below it, in the formation of the well-known plexuses, afterwards giving off its terminal branches to the muscles, integument, vessels of the trunk and extremities, articular capsules, tendons, and bones. As in the roots, so also in the branches of the common trunk, it is seen that the motor twigs contain principally thick fibres, and those destined for the integument and other organs above named, finer ones; ultimately, however, in the terminal ramifications, all the fibres are of uniform size. The fibres of all the spinal nerves appear to run quite distinct from each other, and to present no divisions in the trunks and branches, whilst, in the terminal ramifications of them, divisions frequently occur, and, at all events in certain animals (Mouse, batrachian larva), also reticular anastomoses. They terminate either in loops, or in free prolongations, the latter being the case, particularly, in the *Pacinian bodies*, which are structures composed of numerous concentric capsules separated by fluid, of an oval form, and measuring $\frac{1}{2}$—2‴, found principally in the hand and foot, and which usually contain the termination of a nerve-fibre.

[In the first and last pairs of spinal nerves occasionally only a single root can be perceived, in the former case the motor, and in the latter the sensitive. I have communicated the diameters of all the anterior and posterior roots on the left

side in a male and female body, in the 'Verh. d. Würzb. phys. med.,' Gesellsch. 1850, Heft II, and the transverse sectional areas deduced from these observations are given in my 'Microscopical Anatomy,' § 116. The roots are furnished with a delicate neurilemma, derived from the *pia mater*, and presenting a similar structure, which forms both an external sheath 0·002''' in diameter, as well as internal septa to the individual fasciculi. The contiguous roots frequently *anastomose*, and this is much more usually the case with the sensitive roots; in the cervical nerves in Man in particular, it is found to take place constantly in one or other of the nerves.]

§ 120.

The *structure of the spinal ganglia*, in the Mammalia, is a difficult subject of investigation, but I think the following may be stated with certainty respecting them. The sensitive roots, so far as I have hitherto been able to make out, *enter into no connection with the nerve-cells in the ganglion*, but forming one, or, in the larger ganglia, several, or even numerous fasciculi, which

Fig. 154.

Fig. 154. A lumbar ganglion of a young Dog, treated with soda, and magnified 45 diam.: *S*, sensitive roots; *M*, motor roots; *R.a*, anterior branch of the spinal nerve; *R.p*, posterior branch; in both their composition from both roots is manifest; *G*, ganglion, with the cells and ganglion-fibres, which assist in the strengthening of the sensitive roots traversing the ganglion.

in the latter case anastomose, simply traverse it, to be reunited below the ganglion into a single trunk, which is then immediately blended with the motor root. Most of the nerve-cells themselves appear to be in connection with nerve-fibres, giving off either one or two, or, more rarely, several. These fibres, which I term *ganglion-fibres,* proceed in a preponderating majority, perhaps all of them peripherally, joining and strengthening the perforating root-fibres; so that each ganglion is to be regarded as a source of new nerve-fibres.

[The structure of the spinal ganglia (fig. 154) is a difficult subject for investigation, in Man. No complete results can be obtained from the larger of them, but more may be made out in the smaller or smallest, as in those of the fifth sacral nerve and *n. coccygeus,* which are to be sought within the sac of the *dura mater*, also perhaps in the fourth sacral and first cervical nerves. If a comparative examination be instituted, of the spinal ganglia of the smaller Mammalia (Rabbit, Puppy, Mole, Mouse, Rat), and if not only the scalpel and needle be employed, but if the entire ganglia be examined after the application of acetic acid, and above all, of a dilute solution of soda, with the aid of the *compressorium*, a satisfactory insight into their structure may be obtained. The fibres of the roots of the nerves while passing through the ganglia present nothing at all peculiar, that is to say, no change in size; nor have I ever observed any divisions of them, and I think it may be positively asserted, that such an occurrence, if it take place at all, must be extremely rare, as, notwithstanding that I have specially sought for it, and have been able, in the lower Mammalia, to trace numerous nerve-fibres through the entire ganglion, I have never noticed anything of the sort.

The principal constituents of the ganglia—the *ganglion-globules* or *-cells* [nerve-cells] (figs. 155 and 157), have a distinct outer coat, are for the most part roundish, elongated, or pyriform, usually a little flattened, and measure from 0·012 to 0·036‴, or even 0·04‴; on the average 0·02—0·03‴. The contents are throughout finely granular, and not unfrequently exhibit, in the vicinity of the nucleus, an accumulation of yellow, or yellowish-brown, larger pigment granules, which increases in age, and to which the ganglia are chiefly indebted for their

yellow colour. The *nuclei* measure 0·004—0·008‴, the *nucleoli* 0·0008—0·002‴. These nerve-cells are situated, in the first place, in larger numbers on the surface of the ganglion, between the neurilemma and the perforating radical fibres; and secondly, at all events in Man, in the interior, where they occupy the interstices of the plexus formed by the nerve-fibres. The individual cells are retained in their situations by a special tissue, which also separates them from the contiguous cells and from the nerve-fibres. This tissue appears on isolated cells, as if it formed a special coat to them, and is consequently termed their *external sheath*, but in fact it represents a system of small septa, connected in a complex manner, and pervading the entire ganglion, receiving the separate cells in its meshes, and only more rarely appearing as a definitely bounded coat on individual cells. This structure is evidently to be referred to connective tissue; it presents, however, several forms, which have been, in part, already, properly distinguished by Valentin (Müll. 'Arch.,' 1839, p. 143), viz. 1. in the form of a sometimes homogeneous, sometimes more fibrous substance, with scattered, flattened, roundish nuclei of 0·002—0·003‴; and, 2. in that of isolated elongated, triangular or fusiform cells, measuring 0·003—0·005‴, with nuclei as above, and which sometimes may be supposed to resemble epithelial cells, although, as is evident from a comparison of their different forms, they rather correspond with the developmental cells of connective, or of elastic tissue (fig. 156). Besides these two forms, the former

Fig. 155.

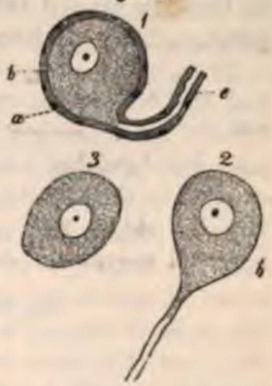


Fig. 156.

Fig. 155. Ganglion-globules (nerve-cells) from the Gasserian ganglion of the Cat, × 350 diam.: 1, cell with a short, pale process, showing the origin of a fibre; *a*, sheath of the cell and nerve-tube, containing nuclei; *b*, cell-membrane of the nerve-cell: 2, cell with the origin of a fibre, without sheath; *b*, cell-membrane of the nerve-cell; 3, nerve-cell, deprived, in the preparation of it, of its membrane and external sheath.

Fig. 156. Cells from the sheath of the nerve-cells of the spinal ganglia in Man, × 350 diam.

of which occurs everywhere, and the latter principally in the larger ganglia, certain intermediate types are met with in Man, which consist, as it were, of nucleated 'fibres of Remak,' as they are termed (*vid. infra*), or, at all events, in the preparation, break up into such.

From by far the greatest number of the nerve-cells, in Man and the Mammalia, are given off pale processes, 0·0015—0·0025‴, in all respects corresponding to those of the central cells, but furnished with a special sheath, and which, as I discovered in the year 1844 ('Selbst. u. Abh. des Symp. Nerv.,' Zürich, 1844, p. 22), are each of them continued into a dark-bordered nerve-tube (figs. 155, 157). The cells observed by me had but one process, the so-termed *unipolar-cells*, and I at first thought that such only existed in the spinal ganglia. It now appears, however, from more recent researches, especially from those of Stannius, that they also contain cells with two processes, one of which may again divide; fresh and more extended investigations therefore are required to show how the matter really stands. At present I think the following should be remarked: 1. in Man and the Mammalia I have certainly established the fact of the existence of unipolar-cells, and think it may also be asserted that they are very numerous; 2. quite lately I have myself, although rarely, noticed cells with two, pale processes, and I am willing to admit the possibility that such cells frequently occur, as it is certain that many processes must be torn off in the comparatively rude methods necessarily employed to isolate the cells; 3. when Stannius very recently noticed in a human fœtus, and in a fœtal Calf, together with unipolar and apolar cells, in the latter numerous *bipolar* cells, it should be inquired whether

Fig. 157.

Fig. 157. Twigs of the coccygeal nerve within the *dura mater*, with an adherent, pedunculated nerve-cell in its nucleated sheath, from which the derivation of a fibre is very distinctly seen, × 350 diam. From Man.

the latter were not cells which afterwards *divide?*—because divisions of the nerve-cells undoubtedly take place (vid. *infra*),—and in this way become unipolar; 4. whether the cells give off one or two fibres, one of the latter does not go towards the centre and the other towards the periphery, but both proceed in the latter direction; at all events, in the examination of all small ganglia, only such ganglion-fibres are visible. Stannius, in bipolar-cells of this kind from the Calf, also found the two processes closely approximated; 5. it is difficult to determine whether cells without processes also occur in the spinal ganglia, seeing that the processes are very readily detached, and that cells thus truncated may very easily be regarded as apolar cells. In small ganglia in the Mammalia a fibre may be traced to each cell, whilst in the smallest spinal ganglia in Man, and in the inconstant ganglia of the posterior roots (vid. *seq.*), cells are not unfrequently met with, to which no fibre is attached, and, consequently, I would, at present, merely state that, in any case, fibres arise from the *majority* of the cells. In order to examine these conditions, either the larger ganglia in Man are selected, which are torn into fibres as carefully as possible under a simple microscope, until the fibres are traced to their origin, which may be done with a little trouble in almost every ganglion, or the small ganglia of the fifth sacral and coccygeal nerves are taken for the purpose. In these ganglia, in almost every individual, solitary and completely isolated, pedunculated, ganglion-globules are met with, close to or in the neighbourhood of the ganglia, each in its special sheath, which in this case appears to be homogeneous (fig. 157), and in many cases, the simple, dark nerve-fibre lying in the peduncle of the globule, and frequently also its connection with the cell, by means of a pale process, may be distinctly perceived. In the *ganglia aberrantia* also of Hyrtl, that is to say the inconstant, larger or smaller collections of nerve-cells, which are found in every subject upon the posterior roots of the larger nerves, the simple origins of fibres may occasionally be distinctly noticed. The dark-coloured fibres, arising from the nerve-cells, simply constitute the continuation of the pale processes of the cells, so that the membranes and contents of each part pass continuously into each other, and thus also the membrane and the contents of the cells are connected with the sheath of the

nerve-tubes, the medullary sheath, and the axis-cylinder. In older nerve-cells, or by the operation of re-agents (arsenious acid, chromic acid, iodine), the contents of the cell become detached from the membrane, and the axis-cylinder appears as a direct continuation of the former (fig. 158), as was first shown by Harting (*vid.* also Stannius in 'Gött. Anzeig.,' 1850, and Leydig, l. c. Tab. 1, fig. 9), which is the best proof that the contents of the nerve-cells cannot be understood as contained in a dilated nerve-tube. The nerve-tubes or ganglion-fibres thus originating, which frequently arch round or embrace the cells with several circular turns, are at first *fine*, measuring 0·0015—0·0025''', but (not continuing so as I formerly supposed, when I was acquainted only with their origin), they all very soon increase in size, as may be very readily observed in many fibres, whilst still within the ganglion, up to 0·003''' and 0·004''', many even to as much as 0·005 and 0·006'''; becoming, consequently, *medium-sized*, and *thick nerve-fibres*.

Fig. 158.

The processes of the cells and the nerve-fibres springing from them are also furnished with nucleated sheaths like the cells themselves, the *vaginal processes*, as they are termed, which they lose, however, at the point where they join the emergent trunk, obtaining instead of it, as a coat, the common neurilemma of the nerves.

The description I have above given of the conditions observable in the spinal-ganglia in Man and the Mammalia, differs very considerably from what was found by Bidder, Reichert, R. Wagner, and Robin, to be the case in Fishes.

Fig. 158. Nerve-cell of the Pike (bipolar, as they are termed), which is continued at each end into dark-bordered nerve-tubes, treated with arsenious acid, × 350 diam.: *a*, sheath of the nerve-cell; *b*, sheath of nerve; *c*, nerve-medulla; *d*, axis-cylinder continuous with the contents of the nerve-cell; *e*, which have shrunk away from the sheath.

The chief difference consists in this, that whilst in the Mammalia, from all we know, the roots of the nerves have no direct connection with the nerve-cells, and merely pass through the ganglion, in Fishes, all the radical fibres are connected with the cells, so that each fibre is interrupted by a bipolar cell, and independent ganglion-fibres are wholly wanting. R. Wagner has thought, that what obtains in the Fish might be applied, unconditionally, to all the Vertebrata, and asserts, that the occurrence of bipolar cells in the course of the posterior radical fibres is in accordance with Bell's doctrine, and a necessary contingent in the mechanism of the sensitive fibres; and moreover, that in this case the highly important and long-sought distinction between sensitive and motor primitive fibres, has been discovered. In opposition to this I have expressed the opinion, that it is not a necessary postulate, that what is found in the Fish should be applied to Man, and that the interruption of a sensitive fibre by a nerve-cell does not distinguish it from a motor fibre. Although Wagner has very recently characterised this opinion of mine as unphysiological, he will not, at the same time, convince any one that the spinal ganglia of the Mammalia are constructed as he thinks, and I shall therefore wait to see whether further observations will confirm my observations or not. In order to complete them, I will moreover mention, that direct measurement of the sensitive roots above and below the ganglia, shows a not inconsiderable difference in favour of the latter situation (*vid.* 'Mikroskop. Anat.,' II, p. 509), which as differences in the thickness of the entering and emergent nerve-fibres, and divisions of them within the ganglion do not exist, can only be referred to the fibres which originate in the ganglion and proceed towards the periphery, a view which is also confirmed by direct observation (fig. 154). With respect to the interesting observations on the structure of the spinal ganglia of the lower animals, and particularly of Fishes, I would refer especially to the works of R. Wagner, Bidder, Robin, and Stannius, cited below.]

§ 121.

Further course and termination of the Spinal Nerves.—Below the spinal ganglion, the sensitive and motor roots unite to form a common trunk, their fibres being intermixed in diverse ways,

as may be very distinctly perceived in small animals. All the subsequent branches, both of the anterior and posterior main divisions, as well as their further continuations, are consequently of a *mixed* nature, formed of portions derived from both roots; a condition which they retain up to their ultimate distribution. Here, however, an alteration takes place, the motor fibres going off in by far the larger proportion into the muscular branches, and the sensitive chiefly to the cutaneous. Where the ganglion-fibres which arise in the spinal ganglia are distributed, cannot be ascertained anatomically. When their physiological relations, however, are considered, it would appear as by far the most probable supposition, that they do not, as at first sight one would be inclined to suppose, join the sympathetic in the *rami communicantes*, but, that accompanying the spinal nerves, they are continued chiefly into the vascular branches, and consequently are distributed in the integuments, muscles, bones, joints, tendons, and membranes (*periosteum, pia mater*, &c.), but also, perhaps, to the glands and involuntary muscles of the skin. The nerve-fibres in the main trunks of the spinal nerves present the same diameter as in the roots, that is to say, there are finer and thicker tubes, and a certain number of intermediate forms; but, as they proceed, the fibres separate, the thicker going more to the muscular branches, and the thinner into the cutaneous nerves. According to the statements of Bidder and Volkman, the proportion of the fine to the thick fibres is, in Man, as 1. 1 : 1, in the muscular nerves as 0. 1—0·33 : 1; statements which I can but confirm, adding to them, that the nerves of the bones contain, in the trunks, one third of thick and two thirds of fine, whilst those of the articulations, tendons, and membranes, exhibit a great preponderance of fine fibres. In my opinion, most of the fine fibres contained in the branches of the spinal nerves must be regarded as derived from the spinal cord, and as being, in their function, quite of equal importance with the thick fibres, and, at present, the only thing that remains unascertained, is whether they all ascend to the brain, or perhaps in part arise in the spinal cord; upon which point reference may be made to § 112.

The spinal nerves are composed in general of parallel tubes, for the most part undulating, upon which circumstance their transversely banded aspect depends; they exhibit,

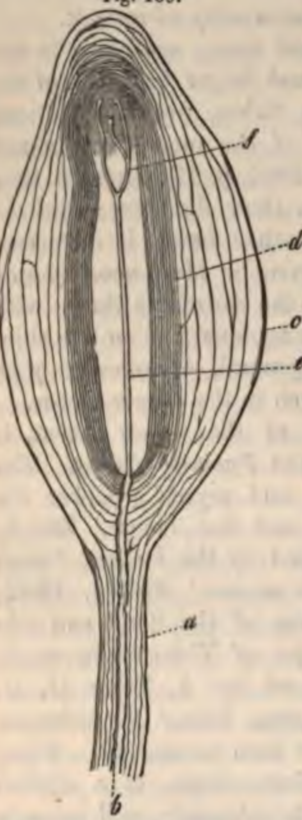
however, in their course, very frequent anastomoses, in which way the various larger and smaller *plexuses* with decussating fibres are formed. The formation of these plexuses is due to an interchange of entire fasciculi or fibres, never to a connection between the individual primitive fibres, and in a microscopical point of view affords no point worthy of remark.

Divisions of the nerve-fibres do not occur, according to our present experience, in the trunks and larger branches of the spinal nerves of the Mammalia [in Fishes, Stannius noticed numerous divisions in the trunks of the motor and mixed nerves ('Archiv für phys.,' Heilk. 1850, p. 77)], nor do they exhibit any considerable change in their diameter; but in the ultimate ramifications, on the other hand, it is certain that such divisions do take place, even in Man, accompanied by a very considerable diminution in the size of the fibres; with respect to which conditions, and the terminations in the skin, muscles, bones, and membranes in general, reference may be made to the detailed descriptions given in the proper places.

One kind, only, of termination of the spinal nerves, is still to be noticed here,—that in the *Pacinian bodies*. The small bodies, so named by Henle and myself ('Ueber die Pacin. Körperchen des Menschen und der Thiere,' Zürich, 1844), were first accurately described by the Italian, Pacini ('Nuovi organi scoperti nel corpo umano,' Pistoja, 1840), especially in the nerves of the palm of the hand and sole of the foot, and, in fact, as Langer of Vienna afterwards showed, had been previously noticed by A. Vater (J. G. Lehmann, 'De consensu partium corp. hum.,' Vitembergæ, 1741), although their nature had not been recognised. These organs are of an elliptical or pyriform shape, of a whitish transparent colour, with whiter streaks internally, and measure $\frac{1}{2}$—2''' in size; in Man, they are constantly found on the cutaneous nerves of the palm of the hand and sole of the foot, in the subcutaneous connective tissue itself, and most numerously in the fingers and toes, particularly on the third phalanx,—according to Herbst ('Die Pacin. Körperchen und ihre Bedeutung,' Gött., 1847) there are about 600 in the hand and not quite so many in the foot; besides which, it must here also be stated, that they are invariably found on the great sympathetic *plexus*, in front of, and close to the abdominal aorta,

behind the *peritoneum*, particularly near the *pancreas*, frequently also in the mesentery, close to the intestine; and also occasionally on other nerves, such as the *n. pudendus communis*, on the *glans penis* (Fick) and bulb of the urethra, on the intercostal nerves, sacral plexus, cutaneous nerves of the upper- and fore-arm, on the dorsum of the hand and foot, and the cutaneous nerves of the neck.

Fig. 159.



The structure of the Pacinian bodies is, upon the whole, simple (fig. 159). Each of them consists of very numerous (20—60) concentric layers of connective tissue, of which layers the external are separated by wider, and the internal by narrower interspaces, in which is contained a clear serous moisture, which is collected in larger quantity in an elongated central cavity, bounded by the innermost lamella. Each body presents a rounded peduncle, formed from the continuations of its lamellæ, and connected with a nervous twig, and in which a dark nerve-fibre, 0·006—0·068‴ (in the Cat, 0·0044—0·0077‴) thick, runs to the Pacinian body. This fibre enters the central cavity from the peduncle, where it becomes 0·006‴ wide and 0·004‴ thick, pale, non-medullated, almost like an axis-cylinder, and terminates in the upper part of the cavity, in a free, slightly granular tubercle, the extremity being frequently bifid or trifid. Further observations, and comparative anatomical details with regard to these bodies, which are also found in great number in many Mammalia, as well as in Birds, in the

Fig. 159. A Pacinian body in Man, × 350 diam.: *a*, its peduncle; *b*, nerve-fibre in it; *c*, external; *d*, internal layer of the sheath; *e*, pale nerve-fibre in the central cavity; *f*, divisions and terminations of the same.

skin, beak, and tongue (Herbst, Will), and with respect to which physiology is still wholly in the dark, will be found in the works above quoted, and also in Reichert ('Bindegewebe,' p. 65), Herbst ('Gött. gel. Anz.,' 1848, Nos. 162, 163, 1850; 'Nachr. v. d. Univ.,' p. 204, 1851, p. 161), Will ('Sitzungsber. d. Wiener Acad.,' Feb., 1850), Osann ('Bericht über d. zoot. Anst. in Würzb.,' 1849), Strahl (Müller's 'Arch.,' 1848, p. 163), and Pappenheim ('Comptes rendus,' xxiii, p. 68). [Todd and Bowman, 'Physiol. Anatomy,' Part II, p. 395, figs. 74, 75, 76; and Bowman, art. 'Pacinian Bodies,' 'Cyc. of Anat. and Phys.']

The spinal nerves, from their point of exit through the *dura mater*, are enclosed by a firm sheath of connective tissue—the nerve-sheath, or *neurilemma*—which also sends finer prolongations into the interior of the nerves, and, as in the muscles, forms boundaries to larger or smaller fasciculi, as well as extremely delicate septa between the individual tubules (fig. 160). In the ultimate ramifications, where isolated primitive fibres, or some few of them, still often retain an external coat, the neurilemma presents the aspect of a homogeneous membrane, with elongated nuclei of 0·003‴; and it presents this character also in the smaller twigs of the cutaneous and muscular nerves, only that gradually the substance begins to split, in a longitudinal direction, into fibres, the nuclei become longer (0·005—0·008‴), frequently almost like those in smooth muscles, and elastic fibres also make their appearance, which are not unfrequently entwined around whole fasciculi. The larger nerves, lastly, present common connective tissue, with distinct longitudinal fibrils, as in fibrous membranes, intermixed with numerous reticulated elastic filaments; they still, however, exhibit, especially in the interior, immature forms of connective tissue.

Fig. 160.

All the larger nerves contain *vessels*, although not in great number; they run principally in a longitudinal direction, and form a loose plexus of minute capillaries of 0·002—0·004‴,

Fig. 160. Transverse section of the ischiatic nerve, × 15 diam.: *a*, general sheath of the nerve; *b*, neurilemma of the tertiary fasciculi; *c*, secondary nervous fasciculi, in part with special sheaths. From the Calf.

with elongated interstices, which invests the fasciculus, and, in fact, penetrates between its elements; never, however, surrounding individual primitive fibres, but only entire divisions of them. The ganglia contain a delicate capillary plexus, in the form of a network, so that each nerve-cell is surrounded by special vessels. The Pacinian bodies also contain vessels, which even penetrate as far as the central cavity (Todd and Bowman, II, p. 397, fig. 75, and p. 399, fig. 76; Herbst, Tab. IV, figs. 1 and 2).

[On the subject of the condition of the cutaneous nerves of animals, I would here add a few remarks. In the skin of the tail of batrachian larvæ (*Rana, Bufo, Triton, Bombinator, Alytes*), I have described the very delicate ramifications and plexuses of the embryonic pale nerve-fibres; and moreover, quite evident loops of the fully formed dark nerve-tubes, and isolated divisions of the latter ('Ann. des S. Nat.,' 1846, p. 102, pl. 6, 7). In the full-grown Frog, according to Czermák (Müll. 'Archiv,' 1849, p. 252), the nerves destined to the skin, form, on its inner aspect, a wide network, already described by Burdach, from which again numerous fasciculi are given off, penetrate the *derma* perpendicularly, and, having reached the superficial glandular layer of the skin, form a superficial nervous-plexus between the glands. With respect to the true termination of the nerve-fibres, Czermák arrived at no definite results, but made the interesting discovery that thick and thin nerve-fibres of the deeper plexus divide dichotomously very frequently and repeatedly, and thus spread themselves over larger surfaces; of which divisions I have most fully satisfied myself from preparations furnished by Czermák. Similar conditions were found by Leydig ('Zeitsch. f. wissen. Zool.,' III) in the skin of Fishes; where also exist superficial and deeper plexuses, with numerous divisions of finer and thicker tubes, all of which on the surface ultimately become quite fine, pale, and finally invisible. In the Invertebrata, as appears from Leydig's researches in *Argulus*, and especially in *Carinaria*, conditions are met with perfectly analogous to those described by me in the nerves of the Tadpole; and I cannot agree with Leydig, when he describes the nucleated enlargements as nerve-cells. On the other hand, the conditions observed in *Artemia* and *Corethra*

are, perhaps, peculiar, because in these instances larger branches of the cutaneous nerves are, at their extremities, in connection with numerous roundish vesicles, which might have the function of nerve-cells ('Zeitsch. f. wiss. Zool.,' vol. I, iii).

In the integuments of the Mammalia and of Man, except in the Pacinian bodies, until a short time since, no one had seen anything of divisions in the nerve-tubes; all observers rather agreeing that terminal loops existed there, especially in the papillæ. But it now appears, from the researches of myself, J. N. Czermák, and C. Gegenbaur, that probably loops and divisions, and occasionally even free terminations, all exist in that situation. That in Man, terminal loops occur in the papillæ, and divisions in the terminal plexuses, I have already mentioned; the latter are especially well shown in the *conjunctiva scleroticæ*, where free terminations also appear to exist, and where peculiar convolutions of nerves (nerven-knäuel), similar to those formerly described by Gerber[1] (*vide* 'Mikrosk. Anat.,' II, i, p. 31, fig. 13 *A*, 3), present themselves. Czermák, moreover, observed divisions of the cutaneous nerves in the Mouse, and I myself a transition of the dark-bordered nerves into pale anastomosing filaments, of 0·001—0·0005‴, exactly resembling the embryonic fibres in the Tadpole ('Mikrosk. Anat.,' II, i, p. 24); lastly, Gegenbaur has noticed numerous divisions in the expansion of the nerves of the tactile hairs in the Mammalia. Further experience will have to show in what relative proportions the loops, divisions, and free terminations, stand with respect to each other, and whether in the different Mammalia, notwithstanding any apparent difference, some correspondence obtains or not.]

§ 122.

Cerebral Nerves.—The sensitive and motor-nerves arising in the brain, correspond in most particulars so closely with the spinal-nerves, that a short description of them will suffice; and with respect to the higher nerves of sense, they will be afterwards described, more fully, in connection with the organs to which they belong.

The motor cerebral-nerves, the third, fourth, sixth, seventh, and twelfth pairs, with respect both to their roots and to their

[1] ['General Anatomy,' translated by G. Gulliver, p. 263, pl. 19, figs. 99, 100.—Eds.]

course and distribution, present exactly the same conditions as the motor-roots and muscular branches of the spinal nerves, with the sole exception, that by all these nerves, from their anastomosing with sensitive nerves, some sensitive fibres are conveyed to the muscles. It deserves remark: 1. that according to Rosenthal and Purkinje, nerve-cells exist in the trunk of the *oculo-motorius* in the Ox, which, however, Bidder (p. 32) was unable to find; 2. that the facial-nerve, in its gangliform enlargement, presents a number of larger nerve-cells, through which, however, according to Remak, only part of the fibres pass (Müll. 'Archiv,' 1841); 3. that according to Volkmann (in Bidder's 'Ganglien-körper,' p. 68), the small root of the hypoglossal nerve in the Calf, which is furnished with a ganglion, produces motor effects. What is the significance of this occurrence of nerve-cells in motor-nerves has not been ascertained. Probably simple fibres having a peripheral destination arise from them, exactly as in the spinal ganglia. In any case it shows that ganglia are not necessarily placed only on sensitive nerves. The fifth, ninth, and tenth pairs, resemble the spinal-nerves, inasmuch as that they all contain motor and sensitive elements. In the *trigeminus* the small root exhibits a preponderance of thick fibres; the larger, numerous fine fibres. The Gasserian ganglion, as well as the smaller ganglionic body seated upon it, contains many larger and smaller nerve-cells of 0·008—0·030‴, with nucleated sheaths, and presents the same conditions, according to my observations, in small Mammalia and in Man, as a spinal ganglion, that is to say, it is simply traversed by the fibres of the greater root, and, from unipolar cells, gives origin to numerous nerve-fibres of medium size, which go to join the emergent branches. Bipolar cells also occur, but, as it appears, in less quantity, and anything that can be said about apolar cells is as applicable here as in the case of the spinal ganglia. The ultimate distribution of the *n. trigeminus* is for the most part similar to that of the cutaneous nerves, and, in particular, the existence of divisions of the nerve-tubes may be distinctly demonstrated in the mucous membranes, as in the conjunctiva at the edge of the cornea, in the ciliary ligament, in the tooth-pulp, and in the papillæ of the tongue. Terminal loops and free terminations appear to exist in the papillæ of the mucous mem-

brane of the mouth and tongue, and in the conjunctiva, whilst in the *cornea*, the extremities of the nerves are quite transparent and pale, and constitute a wide meshed plexus without any divisions. With respect to the ganglia, which are placed on the *n. trigeminus* (*ganglion ciliare, oticum, sphenopalatinum, linguale, supramaxillare*), I find their structure more to resemble that of the sympathetic ganglia, only that they contain a considerable number of larger nerve-cells. The *glossopharyngeus*, although endowed with motor properties, still, according to Volkmann (Müll. 'Arch.,' 1840, p. 488), has no fibres which do not pass through one or other of its ganglia. In its roots, which contain numerous fine fibres, there are, according to Bidder (l. c. p. 30), in the Mammalia, not unfrequently, isolated nerve-cells, often placed free upon it, in which, as in similar cells, on the roots of the *n. vagus*, the giving off of two middle-sized fibres, it is said, may occasionally be readily perceived. The ganglia of the *glossopharyngeus* present the same conditions as the spinal ganglia, that is to say, the radical fibres simply traverse them, and, within the ganglion, fibres arise from cells, which are for the most part unipolar; its ultimate ramification in the tympanic cavity and in the tongue, contains small ganglia, and otherwise corresponds with that of the *n. trigeminus* (*p. major*). In Man, all the roots of the *n. vagus* enter the jugular ganglion, whilst in some of the Mammalia—Dog, Cat, Rabbit, according to Remak (in Frorieps 'Not.,' 1837, No. 54), in the Dog and Sheep, according to Volkmann (Müller's 'Arch.,' 1840, p. 491), but not in the Calf, in which nerve-cells occur in the apparently motor-root, it has also a primary fasciculus, which has no connection with the ganglion. In the *ganglion jugulare* and in the *intumescentia ganglioformis* of the facial nerve, I have not been able to find anything different from the spinal ganglia, only, that the nerve-cells measure occasionally no more than 0·009‴, although it is true that there are also a great many as large as 0·03‴. The ultimate distribution of the nerve exhibits, as Bidder and Volkmann correctly state, a constant kind of separation of thicker and more slender fibres, so that the branches to the œsophagus, heart, and stomach, are composed almost entirely of fine fibres, whilst in those going to the lungs, and in the *laryngeus superior*, the fine are to the thick fibres as 2 to 1; and in the *laryngeus inferior* and the

rami pharyngei, as 1 to 6—10. All these fine fibres are very far from being derived from the sympathetic, as they occur in preponderating quantity even in the roots of the *vagus*, and are also numerous in the *laryngeus superior*. Many of them, moreover, may be nothing more than attenuated or originally finer ganglion-fibres, as they are termed, arising in the ganglia of the *vagus* itself, and which likewise I should not refer to the sympathetic. With respect to the terminations of the *vagus*, reference must be made below to the proper places. The *n. accessorius Willisii*, although perhaps also in part sensitive, has no nerve-cells, and in its distribution and termination, so far as is known, presents nothing peculiar.

[Terminal loops within the trunks of nerves had been already noticed by Gerber, and have lately been described by Valentin in the *vagus* (pectoral portion) of the Mouse and Shrew-mouse, but without their expressing any opinion with respect to their signification. Still more mysterious are the nervous filaments seen by Remak and Bochdalek, coming out from, and again re-entering the brain.]

§ 123.

Ganglionic Nerves.—Under this name, perhaps, is most suitably designated the *n. sympathicus*, as it is termed,—the *sympathetic* or *vegetative nervous system*,—as it presupposes no physiological hypothesis, but simply expresses the fact, which, anatomically, is most apparent to the eye. The ganglionic nerves are neither a wholly independent part of the nervous system (Reil, Bichat), nor a mere section of the cerebro-spinal nerves; but on the one hand, from the very numerous fine nerve-fibres originating in their ganglia—*ganglion-fibres of the sympathetic*,—form an independent system; whilst on the other, they are also connected with the spinal cord and brain, owing to their receiving a smaller number of fibres of the other nerves. Upon comparing the ganglionic nerves with the cerebro-spinal, we find, that the former, as they are constituted from a double source, in a certain respect undoubtedly resemble the latter, which are also formed from ganglionic fibres of the spinal ganglia, and from others proceeding from the cord; but they differ, particularly in this respect, that they

possess a much greater number of independent elements, of ganglia and ganglionic fibres, and enter into much more numerous anastomoses with each other. Consequently, although we appear to be justified from an anatomical point of view, in considering the ganglionic nerves by themselves, still they must not be regarded as something altogether peculiar, seeing that, essentially, every nerve exhibits the same principal elements, and some cerebral-nerves, *vagus, glossopharyngeus,* possess even numerous peripheral ganglia; and moreover, because comparative Anatomy shows that they are produced from the spinal nerves, and Physiology the absence of peculiar functions in them.

§ 124.

The principal trunk of the ganglionic nerves, (*nervus sympathicus*). The *n. sympathicus* in man appears as a whitish, or white nerve, the dark-bordered fibres of which usually run parallel with each other, without divisions or anastomoses, some measuring 0·0025—0·006‴ or even more, and others not more than 0·0012—0·0025‴. These finer and coarser fibres are partially intermixed, partly disposed more in a fascicular manner, the latter being the case near the ganglia of the main trunk and in that part itself. The structure of the ganglia is, in the main, similar to that of the spinal ganglia. Each of them consists: 1. of perforating nerve-fibres, proceeding from one part of the trunk to the other; 2. of a certain number of finer tubules originating in the ganglion; and 3, of numerous nerve-

Fig. 161.

Fig. 161. Sixth thoracic ganglion, on the left side, of the sympathetic nerve of the Rabbit, viewed from behind, treated with soda, and magnified 40 diam.: *T.* 2, trunk of the sympathetic; *R.c*, *R.c*, *rami communicantes*, each dividing into two branches; *Spl.*, *n. splanchnicus*; *S*, twigs of the ganglion with two stronger fibres and finer filaments, probably going to vessels; *G*, nerve-cells, and ganglion-fibres joining the main trunk.

cells; besides these the *rami communicantes* also enter the ganglia, and a certain number of peripheral branches are given off from it. The nerve-cells in the sympathetic (fig. 162 B), present, in all essential particulars, precisely the same conditions as those in the spinal ganglia, only that they are, on an average, smaller, measuring 0·006 — 0·018‴, 0·008 — 0·01‴ in the mean, with less and paler pigment, or even colourless and usually pretty uniformly rounded. As respects the *origin of the nerve-fibres of the main trunk*, it is, in the first place, evident, that they are in great part derived from the *rami communicantes* which arise immediately below the spinal ganglia from the trunks of the spinal nerves; that they are in general formed like the sensitive roots of those nerves (that is, contain a preponderance of finer fibres), and, whether simple or compound, that they are manifestly connected with both roots. From all that has hitherto been made out, the fibres of these connecting branches are derived chiefly from the spinal cord and from the spinal ganglia, and are consequently roots of the *sympathetic*; in a smaller proportion, however, they might be derived from the sympathetic, and joining themselves to the spinal nerves are further distributed peripherally together with them. Having entered the main trunk of the sympathetic, the *rami communicantes*, so far as they are derived from the spinal nerves, almost invariably run, dividing into two or several branches upwards and downwards in it, towards its cephalic and pelvic extremities, being in apposition with the longitudinal fibres of the trunk. In the Rabbit, the fibres of a given *ramus communicans* may very frequently be traced as far as the nearest ganglion and beyond it, in separate peripheral branches, but, in general, the course of the individual fasciculi very soon escapes the eye. It may nevertheless be asserted with great certainty,

Fig. 162.

Fig. 162. From the sympathetic in Man, × 350 diam. *A*, a portion of a grey nerve, treated with acetic acid; *a*, fine nerve-tubes; *b*, nuclei of the fibres of Remak. *B*, Three nerve-cells, one with a pale process.

that they all gradually go off in the peripheral branches of the main trunk, for in the first place all these branches frequently contain, in considerable quantity, the same dark-bordered thicker fibres, as those which are contained in the *rami communicantes*, and secondly their termination or origin is never observed in the main trunk itself; which circumstance is also the principal reason why the *rami communicantes* can be regarded not as branches of the sympathetic, but only as its roots.

Besides the fine and coarser fibres of the *rami communicantes*, the main trunk of the sympathetic contains other fibres in very great numbers, which are dark-bordered, but pale, finest nerve-tubes measuring 0·0012—0·002‴, with respect to which I unhesitatingly assert, that they originate in it, and are in no way continuations of the *rami communicantes*, as has been quite recently supposed, since the discovery of the bipolar ganglion-cells in Fishes. In the Mammalia it is, in fact, extremely easy to prove, by the examination of entire sympathetic ganglia under the careful application of dilute soda and compression, that the great majority of the fibres of the *rami communicantes* have not the slightest connection with the ganglion-cells, but much rather that they simply pass through the ganglia, and ultimately go off in the peripheral branches. Now, as, besides these fibres in the main trunk, numerous other fibres of the finest kind exist, which can in no way be assigned to the *rami communicantes*, it is clear, that they must be structures of entirely new formation. This conclusion appears to be the more legitimate, when it is added, that it is not, as I first and many since have shown, by any means so difficult to demonstrate simple origins of fibres in the sympathetic ganglia of the Mammalia and Amphibia, and that, in the ganglia a considerable portion of fine fibres assume the aspect of so-called convoluted fibres, that is to say, of fibres winding about in various directions through the mass of cells. From what I have seen in the Mammalia and man, the sympathetic ganglia correspond so far with those of the spinal nerves, that they contain a preponderance of unipolar, rarely of bipolar cells, differing, however, in this respect, that apolar cells certainly exist in them in more considerable quantity, and the ganglion fibres arising in them are invariably of the finest kind,

occurring in the peripheral nerves, and probably in most cases, quit the ganglia in various directions. As for a topographical tracing of the various fibres in the main trunk of the sympathetic, with reference to their origin from particular *rami communicantes* and ganglia, and their continuation into particular peripheral branches,—if more be required than what has already been stated—it is not by any means at present to be thought of, but must be reserved for future investigation.

[It has been asserted, that the smaller cells in the ganglia of the sympathetic are different from the larger cells in the spinal ganglia, for instance; and also that they are connected only with fine nerve-tubes (Robin), but this is not correct, as is apparent in part from the observations of Wagner and Stannius; for we find: 1. in the ganglia of the cerebral and spinal nerves of the Mammalia and of man, all intermediate sizes between larger and smaller nerve-cells, and also, occasionally, though rarely, larger cells, measuring as much as 0·03''' in the sympathetic ganglia; and we may also be convinced, 2. that the diameter of the nerve-fibres originating in the first-named ganglia, is not at all regulated by that of the cells, all their ganglion-fibres being pretty nearly of the same size, and which is confirmed also by the bipolar cells of Fishes, where the one fibre arising from the cell is often considerably thicker than the other; in *Petromyzon*, according to Stannius, even six times. Should it be at all supposed that the small cells are peculiar to the sympathetic nerve alone, I must, as above, with respect to the nerve-fibres, remark, that not to mention the ganglia of the roots of the cerebral and spinal nerves, small nerve-cells also occur in situations where there can be no question about the sympathetic, as in the spinal cord and brain, and,—if instances of the same kind in the peripheral nerves be desired—in the *retina* and *cochlea*. At all events, this much is certain, that the ganglia of the ganglionic system of nerves constantly present smaller nerve-cells, and that the fibres arising from them are of the fine kind only.

Bidder and Volkmann have shown, in the Frog, that the greater part of the fibres of the *rami communicantes* are distributed peripherally, with the spinal nerves, and that only a small portion of them, which moreover are derived from the

spinal ganglia, should be regarded as roots of the sympathetic. But I think I have noticed in the Rabbit and in Man, that the *rami communicantes* have chiefly a central destination. Still, in man, fibres also occur very frequently—according to Luschka always,—which must be regarded as branches of the sympathetic going to the peripheral distribution of the spinal nerves, from which again twigs are given off to nerves of the vertebræ; with respect to which conditions the more detailed observations given in my 'Mikroskop. Anatom.,' II, p. 525, and particularly those of Luschka ('Nerven des Wirbelcanals,' p. 10 et seq.) may be consulted. With regard to the question, whence the fibres are derived which join the main trunk of the sympathetic from the spinal nerves, it is certain that that portion of the *rami communicantes*, which arises, from the motor root, and which, according to Luschka, is always a white filament, takes its origin from the cord (or brain) itself, but as regards the other, proceeding from the sensitive root, it may be formed, in part or wholly, from fibres originating in the ganglion. The latter, however, appears to be improbable, for two reasons: 1. because in that case, the existence of conscious sensations from parts supplied by the sympathetic would scarcely be conceivable; and 2. because the fibres originating in the spinal ganglia are of medium size, whilst, in the *rami communicantes*, upon the whole, only a few of that kind occur, and these, moreover, must be referred to the motor root.

We may here offer a few remarks upon the *fine fibres* of the ganglionic nerves. It has been long known, that the sympathetic contains a larger proportion of finer nerve-fibres than the cerebro-spinal nerves, but it was not till 1842 that Bidder and Volkmann laboured to show, that these fibres are not only smaller, but also, in other respects, anatomically different; on which account, in contra-distinction to the thick fibres of the cerebro-spinal nerves, they termed them *sympathetic nerve-fibres*. In opposition to this, Valentin ('Rep.,' 1843, p. 103) and I ('Sympath.,' p. 10 et seq.) have endeavoured to prove, that the fine fibres in the sympathetic do not constitute a special class, and in this I think we were tolerably successful. The principal reasons are as follows: 1. Fine and thick nerve-fibres do not differ intrinsically in any essential respect except in size, and present the most numerous intermediate dimensions. 2. Fine nerve-fibres

having exactly the same characters as those of the so-termed sympathetic exist in many other situations, as for instance,—in Man and the Mammalia,—in the posterior roots of the spinal nerves and of the sensitive cerebral nerves, in which situations, as I have already shown, there can be no question whatever as to a derivation of the fibres from the sympathetic, and where we have, presented to us, nothing but fine cerebro-spinal fibres; similar fibres are contained by thousands in the spinal cord and brain, as well as in the two higher nerves of sense. 3. All thick nerve-fibres decrease in size in their ultimate ramifications, owing to divisions, or direct diminution, so that ultimately they acquire the diameter and nature of the fine, and finest kinds of fibres. 4. All thick nerve-fibres in the course of their development are, at one time, exactly in the condition of the so-termed sympathetic fibres. From these facts it would appear certainly evident, that it is impossible to regard the fine fibres of the sympathetic as altogether of a special nature, and peculiar to it alone, and that it will not do, in the *anatomical* point of view, to classify the fibres according to their size, very many in fact, in their course, assuming all possible degrees of thickness. Allowing that the great number of very fine pale fibres in the sympathetic is a prominent anatomical fact, as is also indeed the case in the higher nerves of sense and in the grey substance, still, speaking physiologically, I am by no means of opinion that the fineness of the fibres in the sympathetic indicates anything of a special nature in them, and which does not exist elsewhere, but perhaps, that where this condition does exist both in them and in other situations, it is connected with a distinct kind of function.]

§ 125.

Peripheral distribution of the ganglionic Nerves.—From the main trunk of the sympathetic arise the branches proceeding to the periphery, which, without exception, receive finer and thick fibres from it, but besides these, in part at least, contain other special elements, to which is due their varied aspect. Some of them, for instance, are white, as is the main trunk in most situations, such are the *n. splanchnici;* others greyish white, as the *nervi intestinales,* the nerves of the unimpregnated uterus (Remak, 'Darmnerven System,' p. 30); others again

grey, and at the same time less firm to the feel, as the *n. caroticus internus*, the *nn. carotici externi s. molles*, the *nn. cardiaci*, the vascular branches in general, the branches connecting the large ganglia and plexuses in the abdomen, those which enter the glands, and the pelvic plexuses. The peculiar condition of the latter nerves depends, in part, upon the paler colour of the fine fibres of the sympathetic itself, but in great measure upon the presence of the fibres, named after their discoverer, the *fibres of Remak* ("gelatinous fibres" of Henle), which were at first regarded as a kind of nerve-tubes, and of which, even now, some cannot be convinced that they are only a sort of connective tissue. They are sometimes more readily isolated, sometimes more united into a compact substance resembling homogeneous connective tissue. In the former case they present the aspect of flat, pale fibres, 0·0015—0·0025‴ broad and 0·0006‴ thick, of an indistinctly striated, granular, or more homogeneous substance; and which, under the action of dilute organic acids, exhibit precisely the same conditions as connective tissue, and from point to point are furnished with, mostly elongated, or fusiform nuclei, 0·003—0·007‴ long, 0·002—0·003‴ broad. These fibres, again, are found in almost all the grey portions of the ganglionic nerves—I cannot find them in many parts of the pelvic plexuses in Man, where they are replaced by a non-nucleated abundant connective tissue, though they are said by Remak to abound in the nerves of the impregnated uterus, ('Darmnervensyst.,' p. 30) in very great quantity, so that they amount to from three to ten times the number of the dark-bordered true nerve-fibres. They constitute the main part of the proper basis of these trunks, and the dark-bordered tubes extend through them, sometimes more isolated, sometimes assembled in larger or smaller fasciculi; more rarely, and only in the neighbourhood of the ganglia themselves, do they appear to form sheaths to individual tubes of the finest kind. Besides these 'fibres of Remak,' the peripheral ramifications of the sympathetic are, above all, distinguished by a great number of *ganglia*. These bodies, of a larger or less size, some even microscopic, are placed on the branches or terminations, and, indeed, the microscopic ganglia, so far as is hitherto known, on the *nervi carotici*, in the pharyngeal plexus, in the

heart, at the root of the lungs and in the lungs, on the supra-renal capsules, in the lymphatic glands, in the kidneys of Man occasionally, on the posterior wall of the bladder, in the muscular substance of the neck of the *uterus* in the Sow, in the *plexus cavernosi*, and with respect to their distribution, will be further adverted to when we come to speak of the viscera. I will here remark, in general, concerning them, that with respect to the size and figure of the nerve-cells, and the origination of fine fibres, they present precisely the same conditions as the ganglia of the main trunk. As regards the last point, it may be especially noticed, that in one situation the origin of nerve-fibres from unipolar cells, and the rarity of the double origin of fibres, is particularly well displayed, viz. in the septum of the heart in the Frog (fig. 163), where R. Wagner has also described their occurrence. These ganglia, therefore, are also sources of nerve-fibres, and the emergent branches always contain more than the roots, on the supposition that the fibres come out only in one direction, which perhaps in most places may be the case. In the same situation also, it is most readily and satisfactorily seen that many of the cells are apolar and without any processes (fig. 163); as is also most plainly shown in the cardiac ganglia and small ganglia on the wall of the urinary bladder in *Bombinator*, in which ganglia, as well as in the similar ganglia in the Frog, the conditions described are as manifest as possible.

Fig. 163.

How the fibres arising from these various localities, from the *rami communicantes*, the ganglia of the main trunk, and the peripheral ganglia, are disposed in their ultimate distribution, is as yet very doubtful. Many peripheral branches anastomose with other nerves, and thus escape all further research, as the *nn. carotici externi* and *internus*, the latter of which, containing scarcely anything but fine fibres and numerous 'fibres of Remak,' I do not look upon in the common sense as a root, but as a branch, arising from the superior cervical ganglion, and probably the other cervical ganglia; as well as

Fig. 163. Nerve-cells from the cardiac ganglia of the Frog, × 350 diam.; one with the origin of a nerve-tube.

the *rami communicantes*, seeing that individual fibres of them, actually join peripherally the spinal nerves; and the *rami cardiaci, pulmonales*, &c. Other branches in the parenchyma of the organs become so fine, that it is impossible to trace them. What has been as yet established respecting their ultimate course, is as follows: 1. *Divisions occur in the branches and terminal ramifications of the sympathetic*, as in the nerves of the spleen, the Pacinian bodies in the mesentery, in the nerves accompanying the mesenteric vessels in the Frog, in those which exist temporarily in the uterus of the Rodentia, of the lungs and stomach of the Frog and Rabbit, of the dura mater on the meningeal arteries, in branches of the sympathetic of the Sturgeon, in the cardiac nerves of the Amphibia, and in those of the urinary bladder in the Rabbit and Mouse. 2. *There are free terminations of the nerves*, as in the Pacinian bodies and on the mesenteric vessels in the Frog. 3. *The thicker fibres of the sympathetic ultimately so decrease in size, as to become of the fine kind*; as may be readily seen in the *rami intestinales, lienales*, and *hepatici*, which, indeed, even in the interior of the organs in question, contain some coarser nerve-fibres, but ultimately lose them. The actual terminations, however, in the organs themselves, in the heart, lungs, stomach, intestine, kidneys, spleen, liver, uterus, &c., are as yet quite unknown; although from the impossibility of finding any dark-bordered fibres in the ultimate ramifications of these nerves, it may be supposed that they terminate, almost everywhere, in non-medullated, embryonic fibres. In fact, I have, at all events hitherto, in vain endeavoured to find a trace of them. Schaffner says, that in the heart of *Bombinator* he has seen the passage of the dark-bordered fibres into pale, anastomosing fibrils of the *finest kind*, whilst Pappenheim (l. c.) describes loops in the nerves of the kidney.

[As regards the nature of the "fibres of Remak," most, recent observers incline to the opinion first advanced by Valentin ('Repert.,' 1838, p. 72; Müller's 'Archiv,' 1839, p. 107), that they are not nerve-fibres at all, but to be referred to the connective tissue of the nerves; whilst Remak still thinks himself obliged to adhere to his previous opinion, that they are, or may be, in part at least, nerve-fibres ('Darmnervensyst.,' p. 30). As

for myself, I freely acknowledge the force of the reasons adduced by the latter observer, which are based chiefly upon the similarity of the fibres in question to the pale embryonic nerve-fibres, inasmuch as that even in the adult, nucleated nerve-fibres are met with in the olfactory nerve; but I am compelled, nevertheless, as before, fully to concur with Valentin, as do also Bidder and Volkmann, and many others. My reasons are the following: 1. The "fibres of Remak," as may be easily shown, arise from the sheath of the nerve-cells of the sympathetic ganglia, and are continued in the nervous trunks, surrounding the nerve-fibres arising from the ganglia. Now as it is certain that these sheaths are a sort of connective tissue, as is apparent also from the spinal ganglia, where they occur in precisely a similar way, only more scantily and without their being continued into the nerves, it follows that the "fibres of Remak" can scarcely be anything else. 2. The finest twigs of the spinal nerves also exhibit nucleated fibres, in all respects like those of Remak, as for instance, those going to the skin, &c.; with respect to which, as they are wanting in the trunks of the nerves, there can be no question at all of their not being nerve-fibres. 3. The quantity of the "fibres of Remak" always diminishes towards the finest ramifications, which could not be the case were they nerves. It is not, indeed, altogether correct, as stated by Valentin, that they are not to be found in the finer intestinal nerves, for there can be no doubt that they do exist there, though much more rarely than in the trunks of the nerves, and are only to be brought into view by compression. According to Remak (Müll. 'Arch.,' 1844, p. 464), they also exist in the cardiac nerves of the Mammalia; although as far as I can perceive, only in the immediate neighbourhood of the ganglia. Relying upon these reasons, I continue in the firm persuasion that the nucleated fibres in the sympathetic nerve of adult Mammalia are a form of the neurilemma; but I will not omit to remark, that I consider it quite impossible to determine, in undeveloped nerves, what is neurilemma and what young nerve-fibres. Thus in the Rabbit, 2—6 months old, in the *n. caroticus internus*, not a single developed nerve-fibre is to be met with, and apparently nothing but "fibres of Remak," although it is quite certain that together with them, there must also exist the rudiments

of numerous dark-bordered fibres. In the nerves of the spleen, in the Calf, in like manner, numerous nucleated fibres are met with, though in the terminations (*vide* 'Cyclopædia of Anatomy,' III, p. 795, figs. 539 and 540), which, probably, afterwards become nerve-fibres. *In young animals, consequently, we must not look for a decision of the question;* whilst in older ones, it is quite otherwise. *In them, a nucleated fibre can only be regarded as nerve when it can be traced into a dark-bordered fibre, or to a true process of a nerve-cell;* and this, as we have seen, is not the case in those of the sympathetic system. It may, however, be remarked, that "fibres of Remak" also occur in the ganglia of the main sympathetic trunk, but that they do not, for the most part, extend to any distance beyond them, so that usually but few are contained in the trunk of the nerve itself.]

§ 126.

Development of the elements of the Nervous System.—The nerve-cells, wherever they may occur, are nothing else than transformations of the so-called embryonic-cells; some of which simply enlarge, whilst others throw out a varying number of processes, and are, at all events in part, connected with nerve-fibres.

Many nerve-cells also appear, at a subsequent period, to increase by division; at all events, I do not know how otherwise to explain the frequent occurrence of two nuclei in the nerve-cells of young animals, especially in the ganglia; and the cells connected by communicating filaments, which have been noticed by various observers.

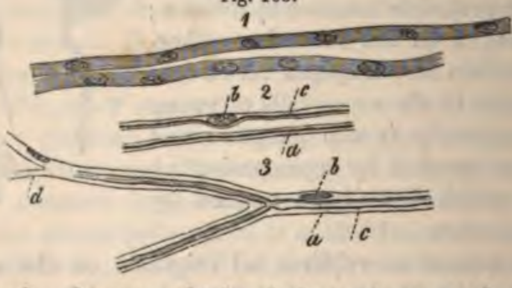
Fig. 164.

The *peripheral nerve-fibres* all originate on the spot, but their subsequent development proceeds in such a way that the central extremities always precede the peripheral. With the

Fig. 164. Nerve-cell from a spinal ganglion of a sixteen-weeks' human embryo: *a*, nucleus in the pale process of the cell; 2, self-developing nerve-tubes from the brain of a two-months' human embryo; 3, cells from the grey cerebral substance of the same embryo.

exception of the extremities of the nerves, they are developed from fusiform nucleated cells, which are nothing else than modifications of the primordial formative cells of the embryo, and are conjoined into pale, flattened, elongated, nucleated tubules or fibres 0·001—0·003‴ broad. Now, at first the nerves consist only of fibres of this kind, and of the rudiment of the neurilemma, being grey or dull white, like the sympathetic filaments; subsequently, in the human embryo at the fourth or fifth month, they always assume a whiter colour, and the proper white or medullary substance continues to be more and more developed in them. Of the three possible modes of development of this substance propounded by Schwann, one only, in the present state of things, can come into question, that namely, as to whether the medullary sheath is a structure deposited between the membrane and the contents of the embryonic nucleated fibres; in which case the contents of the latter would become the axis-fibre. But besides this, the medullary sheath may originate in what did not occur to Schwann, viz., a chemical metamorphosis of the external portion of the contents of the embryonic-fibres; and the axis-fibre may be only the remainder of those contents which has not undergone a fatty metamorphosis. It is difficult to determine which of these two views is correct. Direct observation shows only this much, that the contents of the pale embryonic fibres

Fig. 165.



invariably, by degrees, obtain dark contours, and ultimately present the aspect of a true dark-bordered fibre, whilst it

Fig. 165. 1, two nerve-fibres from the ischiatic nerve of a sixteen-weeks' embryo; 2, nerve-tubes from a newly-littered Rabbit; *a*, their sheath; *b*, nucleus; *c*, medullary sheath: 3, nerve-fibre from the tail of the Tadpole; *a*, *b*, *c*, as before; at *d*, the fibre retains its embryonic character; the dark-bordered fibre shows a division.

teaches nothing with respect to the proper origin of the white substance. Since, however, it can be proved, that the fibres, whilst they undergo this change, do not alter in size, the supposition I have expressed would still appear the more correct.

The development of the *terminations of the nerves,* which appears in some respects to present conditions different from those exhibited in the trunks, may, as I have shown ('Annal. d. sc. nat.,' 1846, p. 102, tab. 6, 7), be readily traced in the tails of the larvæ of the naked Amphibia (fig. 165, 3; fig. 166). We there find, as is mentioned by Schwann (p. 177), the primary rudiments of the nerves to be pale branched fibres, measuring 0·001—0·002‴, which here and there anastomose, all finally terminating in free fibrils of the finest kind, measuring 0·0002 — 0·0004‴. There is no difficulty in showing that these fibres arise from the coalescence of fusiform or stellate cells, for, in the first place, such cells may be seen, in part still in close apposition with, but independent of them; in part more or less connected by means of their processes; and, secondly, cell-nuclei occur at the divisions of the fibres, which are there somewhat dilated; and, at all events in young larvæ,

Fig. 166.

Fig. 166. Nerves from the tail of a Tadpole, × 350 diam.: 1, embryonic nerve-fibres, in which more than one dark-bordered tube has become developed; 2, similar fibres containing but one tube, which in one fibre ceases at *b*; 3, embryonic pale fibres; 4, fusiform cells connected together, and with a complete nerve-fibre.

with them are associated the well-known angular vitelline corpuscles, with which, at first, all the cells of the embryo are filled. At first the number of pale embryonic nerves is very small, and limited to a few short trunks closely applied to the muscular structures in the tail; but they are gradually developed, in the direction from the centre towards the periphery, further into the transparent portion of the tail, new cells being continually added in connection with the existing trunks, whilst the latter themselves, almost in the same manner as the capillaries of these larvæ, unite directly by delicate off-sets. When these fine ramifications—with respect to the nervous nature of which no doubt can be entertained, as it is evident that the larvæ in which they exist already possess very acute sensibility—are once formed, the following further changes then take place. Whilst the fibres gradually enlarge to twice or four times their original diameter, there are by degrees developed in them, and in fact from the trunk towards the branches, dark-bordered, fine primitive fibres, which in no case owe their origin to newly added medullary sheaths, but are certainly formed solely from a metamorphosis of a part of the contents of the pale fibres. In connection with this, however, the following conditions, which have not yet been observed in the higher animals, are to be remarked: 1. where a pale embryonic fibre bifurcates, there occasionally, though not always, also takes place a division of the dark-bordered tube developed within it; 2. the dark-bordered tubes scarcely ever completely fill the pale fibres in which they are formed, but a space, frequently of the same diameter as that of the tubes, is most usually left between them and the membranes of the embryonic fibres, in which space occasionally the nuclei of the primordial formative cells may be perceived; 3. in the trunks and main branches of the embryonic fibres, several (2—4) dark-bordered tubules are undoubtedly developed within one and the same embryonic fibre; a very remarkable condition, which shows that there are even dark-bordered fibres which do not possess a structureless sheath (*vid.* note to § 110), and resembling what exists in the muscular fasciculus, in which, in like manner, within a single tubule, numerous finer elements are produced. As the tail of the Tadpole is afterwards thrown off, it is to be regretted that its interesting nerves cannot be traced to the

same state of completion, as can be done in those of other situations. It is obvious, however, in the oldest Tadpoles, that the nerves are somewhat thicker than they are originally, and that they extend towards the periphery, sometimes in loops, sometimes with free ends, but in such a way that the primary pale fibres continue to exist, and, proceeding from the dark-bordered fibres, constitute a very fine terminal nervous-plexus, with anastomoses and free ends.

I should not have delayed so long on the subject of the nerves in the Tadpole, did not similar conditions most probably also obtain in many other terminations of nerves. This is certain as regards those of the electric organ of the Ray, which, even when developed, agree in many respects with those of the more advanced Tadpole, and as Ecker has lately shown ('Zeitsch. für wissensch. Zoologie,' 1849, p. 38), are developed in precisely the same manner. The nerves, also, in the skin of the Mouse (*vid.* note to § 121), evidently belong to the same category; and consequently it may hereafter be shown, that wherever peripheral divisions of nerves occur, their development proceeds essentially as it is here described.

With respect to the *development* of the *nerve-fibres* in the *central organs*, we possess but few researches. Of the fibres in the ganglia, I can only observe, that they are developed subsequently to those of the nerves, and probably from smaller fusiform cells, which may be noticed in association with the nerve-cells. On one occasion, in a spinal ganglion of a four months' human embryo, I noticed a cell of this kind in connection with the process of a nerve-cell (fig. 164). The formation of the fibres in the cord and brain is extremely difficult of investigation, and is best studied with the aid of chromic acid. In the human embryo, I find, as early as the end of the second month, the commencement of the formation of the tubules in question, the white substance being distinctly finely striated, and manifestly containing, in places, very delicate fusiform cells, which are sometimes independent or isolated, sometimes connected, two or three, or several together (fig. 164). All these cells are at first pale, investing the nucleus, which measures 0·002—0·003''' quite closely, and having processes almost as fine as the fibrils of connective tissue. In the fourth month, when the two kinds of substance

are quite distinct, nuclei are still occasionally to be seen in the now wider fibres, but in some they have disappeared, although the fibres are without dark contours; which are not developed before the middle period of fœtal life (in the fœtal Calf, when more than 12″ long, according to Valentin), and, indeed, first in the spinal cord.

As regards the subsequent changes in the nerve-fibres, it has already been remarked, that they occasionally increase very considerably in thickness. According to Harting (l. c., p. 75), the fibres of the median-nerve which have not yet acquired dark contours, measure in a four months' human embryo, on the average $3{\cdot}4^{m.m.}$, in a new-born child $10{\cdot}4^{m.m.}$, in the adult $16{\cdot}6^{m.m.}$. The increased thickness of the nerves themselves appears, according to Harting, from the fourth month onwards, to depend solely upon the enlargement of the already existing elements, the fœtus and new-born child already possessing the same number of primitive fibres as the adult.

[It remains to be observed, that extremely few *pathological* changes of the nervous elements are known. In the nerve-cells of the brain, the deposition of pigmentary matter becomes excessive, particularly in old age; and fatty deposition also takes place (Virchow, 'Archiv,' I, 1). Valentin thinks that he has observed a regeneration of nerve-cells in the superior cervical ganglion of the Rabbit. Nerve-fibres are readily destroyed, as in consequence of extravasation of blood, tumours, softening, fibroid growths, &c., in which cases the medullary substance breaks up into larger or smaller, coagulated or fluid masses, of very various configuration, whilst the axis-fibres seem to disappear. In *atrophied* nerves, the fibres are observed to be thinner, easily broken up, and, instead of the medullary matter, are frequently, in parts, entirely occupied by minute fatty molecules, as was seen on one occasion by Virchow, in a human optic nerve, and by myself in the nerves of a Frog. Nerves that have been cut across, readily unite; portions of peripheral nerves from 8—12‴ in length, even, are restored by true nervous tissue (Bidder, l. c., p. 65; Valentin '*de funct. nerv.*,' p. 159, § 323; and '*Phys.*,' 2 Aufl. I, 2, 716). Should the union of a divided nerve not take place, the peripheral end undergoes a gradual change in a particular way,

with a simultaneous extinction of the nervous activity. The nerve-fibres generally become yellowish, soft, lacerable, and lose their transversely banded and glistening aspect. They no longer present any trace of a double contour, their medullary substance is wholly coagulated, and their breadth frequently very various (Stannius in Müll. 'Arch.,' 1847, p. 452). Whether the axis-fibres undergo change, we are, unfortunately, not informed. According to Brown-Séquard, incised wounds, even of the spinal-cord, in the Rabbit, united. *Hypertrophies* of the nerve-substance itself are unknown, although probably such a condition occurs in the neurilemma. Virchow noticed a new formation of fine nerves in pleuritic and peritoneal adhesions, and, according to the same observer, it would appear that grey nerve-substance may be formed on the walls of the cerebral ventricles.]

§ 127.

With respect to the *functions* of the nervous system, the following remarks which are immediately pertinent to the anatomical facts—may suffice. As regards the two elementary portions of the nervous system, anatomical investigation shows, that all its divisions, which preside over the higher functions, contain grey substance in greater or less quantity, as in the sympathetic, the ganglia of the spinal and cerebral nerves, and in the spinal cord and brain; whilst the nerves, which act only as a conducting apparatus, contain nothing but nerve-fibres. This being admitted to be the attribute of the grey substance, it may further be inquired whether it presents differences in its structure, as it does in its functions. With respect to this I would remark as follows: the largest nerve-cells are met with in situations from which motory effects proceed, as in the anterior horns of the spinal cord, amongst the fibres of the anterior roots, in the *medulla oblongata,* at the points of origin of the motor cerebral nerves, in the cortical substance of the *cerebellum,* the *pons Varolii,* and *crura cerebri;* whilst the smallest cells are found in the sensitive regions, as in the posterior horns of the spinal cord, the *corpora restiformia,* and *quadrigemina.* There does not however, appear to be any constant relation between the size of the cells and the existence of sensitive or motor functions, for, in the ganglia of the cerebro-

spinal nerves and of the sympathetic, and in the optic *thalami*, both sorts of fibres arise, in one place, from small, and in another from large cells. It seems, therefore, as in the case of the nerve-fibres, that there are large and small motor cells, as well as sensitive cells of various dimensions, a fact which is confirmed by comparative anatomy, as the large bipolar cells in Fishes are manifestly sensitive. No essential difference can be pointed out between sensitive and motor cells, whether the latter be of uniform or of different size, and in particular the variations existing between such cells are not greater than those between the motor cells in different localities. Even the cells in the cortical substance of the brain, to which Physiologists assign the mental manifestations, with our present means of research, exhibit no perceptible peculiarities. The nerve-cells, however, may be divided into those which are in direct connection with nerve-fibres, and those which are not thus connected, but independent. The former, of course, are to be especially regarded as sensitive and motor, with respect to the latter, anatomy to some extent affords no information, inasmuch as, that they present no processes, as in the sympathetic ganglia, and in some situations in the brain; as regards those furnished with processes, particularly the many-rayed cells, which in many situations undoubtedly are not prolonged into nerve-fibres, it might be considered certain that they,—both larger and smaller, by means of their processes which fulfil the functions of nerves, and whether the latter anastomose or not,—bring different regions of the central organs into mutual connection, and participate in the reflex phenomena, the sympathies, and other modes of association of the functions. Cells of this kind exist in the spinal cord and brain everywhere in very large quantity, but not in the ganglia, although it is not, from this, intended to imply that no reflex actions are performed in those bodies.

Respecting the *nerve-fibres*, anatomy is not in a condition to point out any difference in them, between the sensitive and motor nerves; a circumstance, however, which, physiologically, can afford no reason to ascribe identical functions to them. As regards the various sizes of the nerve-fibres, the numerous changes in diameter, undergone in their course by all the cerebro-spinal nerves, very obviously indicate that these proportions have no relation to the functions of the fibres in

general. Nevertheless, I do not look upon these relations of size as altogether of little consequence, and in particular does the attenuation of the fibres, where they extend through grey substance (*vid. sup.*, § 112), appear to me to be important, as also their diminution at their origins and terminations. It is, however, difficult to perceive the physiological import of these facts. Were it the case, that in the nerve-fibres the axis-cylinder alone was the conducting, and the medullary-sheath, an insulating substance, and could it be proved that the medullary sheaths were wanting in the attenuated portions, the peculiar activity of the nerve-fibres in these situations (the transverse conduction in the spinal cord, the acuteness of sensibility at the terminations, &c.) would be satisfactorily explained. It is well known that such a notion has already been entertained by various writers, and its conception has usually proceeded upon the idea that a close alliance or identity exists between electricity and the nervous force, and the medullary sheath abounding in fatty matter, has from this point of view been regarded as an *insulator*. But (1.) it is anything but demonstrated, that the nerves possess no other active force but electricity; and (2.) there is nothing to indicate an absence of the medullary sheath, and a free condition of the axis-fibres in many peripheral extremities of the nerves (skin, muscles), and in those portions of the central organs (spinal cord) in which a transverse conduction is evident. The question always remains, whether the medullary sheath, although not altogether, yet at all events partially, may not insulate more or less, according to its thickness. Since, however, this membrane is wanting not only in many terminations of nerves, where an insulated conducting faculty might not be required, but also in other situations, as in the Invertebrata and the nerves of *Petromyzon* generally, as well as in the processes of the nerve-cells which certainly act as nerves, in the central organs of the higher animals, and in the finest nerve-fibres in those situations (brain), the notion that such is its effect in the dark-bordered nerves loses all ground of support. It would seem to me, that the medullary sheath represents nothing more than a *protective soft envelope for the tender central fibre.* This mode of explanation also, renders it intelligible, why it is, that in dark-bordered nerves, where the medullary sheath is thin or wanting, and the central fibre is in

a more free condition, the nerve-fibres are more readily excited and able to communicate their conditions; and as regards the pale nerve-fibres, in this case they would essentially have the same functions as the others, and the absence of the medullary sheath in them could either be explained on the supposition, that they are less readily excitable, as in the invertebrate animals, and the *Cyclostomata*, or because they occur in situations where a protective tunic to the nerve-fibres is no longer required, as in the *retina*, in the nasal mucous membrane, in the grey substance, and in the electric organs, or even where its refractive power upon light would be prejudicial to a certain object, as in the *cornea*. A similar mechanical function appears to me to be performed by the fine granular substance, which in the higher central organs is found in so many situations supporting the most delicate nerve-fibres, cells, and processes.

[With respect to the methods to be employed in *investigations* of the nervous system, the principal have been noticed in the preceding sections. I will, here, once more advert to the importance of preparations made with chromic acid in the investigation of the course of the fibres, and in the examination of the central nerve-cells; and direct attention to the dilute solution of *caustic soda* for the detecting of nerve-fibres in non-transparent tissues,—without which two means very many points would remain in the dark. In this way also the extreme proneness to become changed, of the grey and white substances, and particularly the ready disruption of the processes of the nerve-cells, and the varicosity, coagulation, and destruction of the nerve-fibres, are at once removed or avoided. The brain and spinal cord, as well as the elements of the ganglia, are best studied in the human subject, but the course of the fibres in them, and, above all, the terminations of the nerves, are best investigated in the smaller Mammalia, and only in the second place in Man. In the searching for the minute ganglia in the heart, Ludwig recommends the treatment with phosphoric acid and the solution of iodine in hydriodic acid, the latter so diluted that it has only a tinge of brown. For the development of the nerves, the human and mammalian embryo are quite suitable; but the batrachian larvæ, and if opportunity offer, the electric

organs of the embryo Ray, in which the conditions are by far the most clearly displayed, should not be overlooked.]

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END OF VOL. I.

C. and J. Adlard, Printers, Bartholomew Close.